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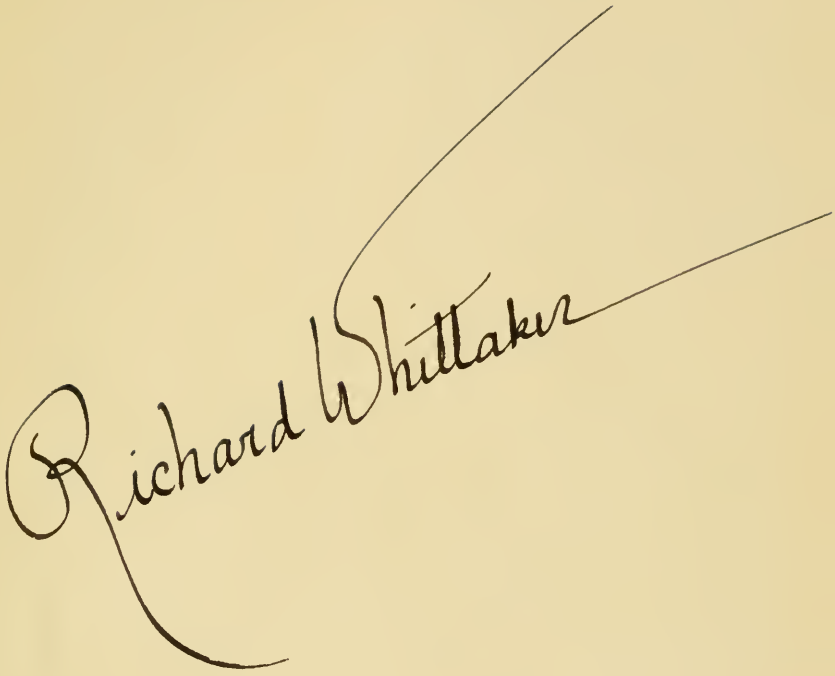

The Wistar Institute
September, 1971.

BIOLOGICAL LECTURES

DELIVERED AT

THE MARINE BIOLOGICAL LABORATORY OF WOOD'S HOLL

1896–1897

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FIRST LECTURE.

THE VARIATIONS AND MUTATIONS OF THE INTRODUCED SPARROW. *PASSER DOMESTICUS.*

(*A SECOND CONTRIBUTION TO THE STUDY OF VARIATION.*)

HERMON C. BUMPUS.

In the preface to the second volume of these Lectures it is stated that one of the leading objects of the course is "to bring forward the *unsettled* problems of the day, and to discuss them freely." The question of the adequacy of natural selection is one that at the present time still divides two schools of speculative biology, and is a question that can be solved only by those inductive methods which it is the function of a Biological Laboratory to suggest, adopt, and execute.

The principle of "Panmixia," or the "suspension of the preserving influence of natural selection," has formed an integral part of the speculative writings of Weismann, and, as part of his theory of "the continuity of the germ-plasm," is presumed to explain adequately the reduction of useless organs, and the occurrence, especially among domesticated animals, of "the greater number of those variations which are usually attributed to the direct influence of the external conditions of life."

This view of the regressive power of natural selection was, at the time of the original presentation of Weismann's essay ('83), not entirely new to science. Lankester ('90) calls attention to the fact that, eleven years earlier, in 1872, Darwin, in the sixth edition of the *Origin of Species*, had the identical principle in mind when he wrote: "If under changed conditions of life a structure before useful becomes less useful, its

diminution will be favored, for it will profit the individual not to have its nutriment wasted in building up a useless structure." Shortly after this Romanes advanced a not totally dissimilar idea in his theory of the "Cessation of Selection" ('74).

In 1890 Romanes revised his earlier views, calling especial attention to the points in which they differed from those of Darwin and Weismann, and in 1895, in his posthumous work, the salient features of his theory are again indicated. Cope carried the application from structures to species when he wrote ('96): "In other cases it is to be supposed that extremely favorable conditions of food, with absence of enemies, would have occurred, in which the struggle would have been *nil*. Degeneracy would follow this condition also."

But, without entering into the conflicting claims of originality and of priority, all the disputants are agreed that the withdrawal of the supporting influence of natural selection from an adapted organ or organism must or may, directly or indirectly, lead to a condition of degeneration. That the arguments, however, are too speculative in character is generally admitted, and there is consequently demand for inductive evidence to prove :

(1) That in a specific case, and in respect to certain characters, the operation of natural selection has been suspended.

(2) That, when the operation of natural selection has been suspended, increased variation occurs.

(3) That, on the occurrence of (1) and (2), there is a departure from a previously maintained and presumably high standard, and

(4) That, unless a new equilibrium is established by adaptation to the new environment, degeneration and perhaps final elimination ensues.

It would also be of incidental interest to learn from observed facts whether the suspension of the action of natural selection is felt immediately by an organ or organism; whether there is any indication of "self-adaptation" tending to the establishment of a new equilibrium; and whether this self-adaptation, if detected, follows one or several definite lines. Of course, if the evidence can be gathered from animals in a state of nature, and if it can be checked by a large number of examples, so much the better.

In 1850 the first house sparrows of Europe were introduced into this country, and from that time to 1870 upwards of 1500 birds are said to have been brought from the Old World (Merriam-Barrows, '89). To these introduced birds the environment has been novel. They have found abundant food, convenient and safe nesting places, practically no natural enemies, and unrivaled means of dispersal. Aside from an early and brief period of fostering care, they have been left to shift for themselves; natural agencies have since been at work, and in the relatively short space of forty years a continent has been, not merely invaded, but inundated by an animal which, in its native habitat, has been fairly subservient to the regulations imposed by competing life.

It seems to the speaker that here is an excellent example of the suspension of natural selection, for here, at least as far as certain external factors of selection are concerned, Nature does not select. Nearly all the young birds reach maturity; variations in color and structure, unless most extreme, are apparently not disadvantageous to their possessor; and if these variations are heritable, they do not seriously handicap the individuals of the next generation. A considerable departure in nesting and breeding habits does not jeopardize the domestic interests, and the simple mode of life permits even the weak individuals to endure. We conclude, then, that there is evidence to prove the first proposition, *viz.*, in a specific case and in respect to certain characters, the operation of natural selection has been suspended.

For a proper discussion of propositions 2, 3, and 4, it was my first purpose to collect a large number of the American birds and compare them directly with an equal number collected in England; but the labor and expense involved made this procedure inexpedient. The egg of the bird, however, is easy to secure, readily preserved, and can be purchased from European dealers for a relatively small price. It presents a remarkable range of variation, both in shape, size, and color, and offers certain fixed and readily measurable features which are not presented by the bird itself. Moreover, my observations lead

me to think that it is a structure which indicates departures from "normality" in a remarkable way. At all events, the variations, though they may present greater amplitude, are of the same inductive value, qualitatively, as variations of the skeleton, feathers, or other adult structures. The egg may be taken, then, as a convenient and inexpensive means for the solution of at least some of the questions bearing on the subject of Panmixia.

At first, one hundred eggs, imported from an English dealer, were compared with an equal number collected in Providence, R. I. The dissimilarity in the two lots of eggs was so striking that I felt there must be some mistake, and at once imported another hundred from a different locality, collecting in the meantime a second hundred of American specimens. On comparing the two enlarged collections, such interesting variations were found that I ordered all the English eggs that could be procured, and collected extensively from certain localities at home. At the close of the summer, 1896, I had 1736 eggs, one half of which were European, the other half American. These eggs, 868 foreign and 868 native, were compared (*a*) with respect to length, (*b*) ratio of length to breadth, (*c*) general shape, and (*d*) color. These comparisons ought to reveal any tendency towards increase of variation on the withdrawal of natural selection, that is, they ought to yield evidence in support of the second proposition. The data may be conveniently arranged in "curves of frequency."

If we erect on a base line (Diagram I), extending from 18 mm., which represents the shortest egg, to 26 mm., which represents the longest egg, a series of ordinates representing in sequence the added increment of ½ mm., and arrange on these ordinates the eggs that measure respectively 18 mm., 18.5 mm., 19 mm., 19.5 mm., etc., it is evident that the mean ordinates will be occupied by a considerably larger number of specimens than the extreme, and that the ascending and descending curve will indicate the general plan of the distribution of variation around the mean. Now if a species or structure is stable and shows only a slight tendency to vary, the base of the curve obviously will be short. If, on the con-

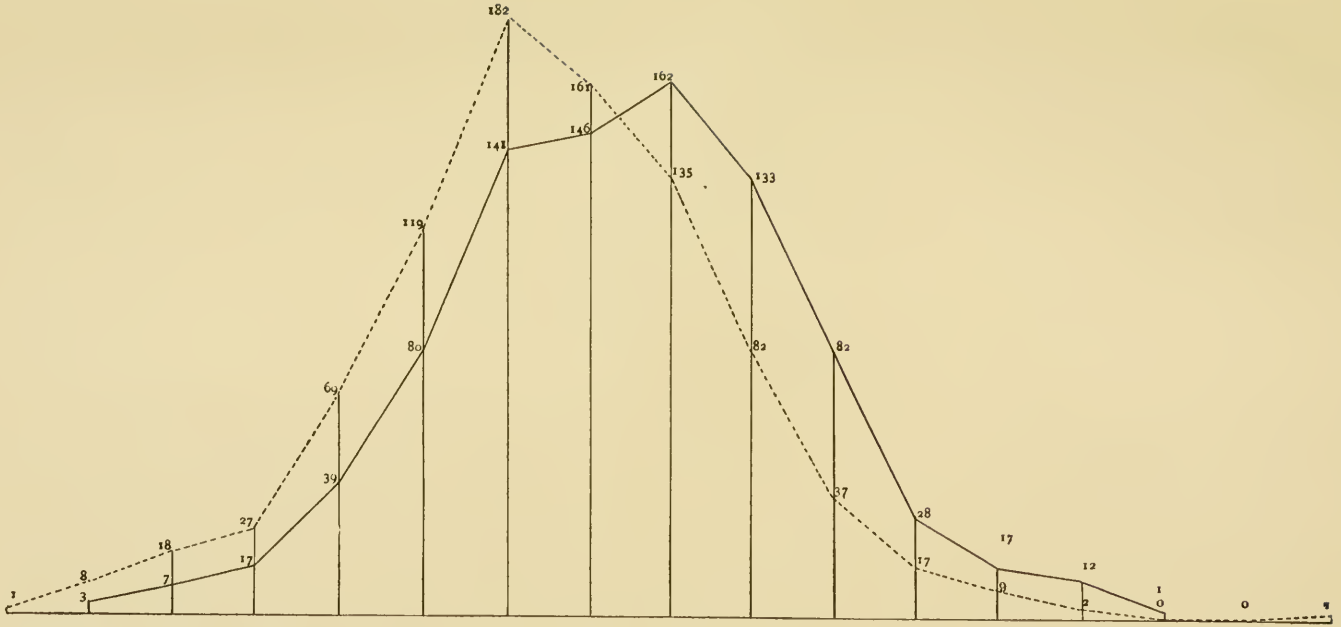

DIAGRAM I. *Curves of Absolute Lengths.* — The distribution of the American eggs is represented by the broken line; that of the British eggs by the unbroken line. The short eggs are at the left, the long eggs at the right. The number of specimens of each length is represented by the height of the respective ordinate; thus there are 80 British and 119 American eggs which have a length of 20.5 mm.

trary, a species is unstable and has a general tendency to vary, the base will be long.

The 868 American eggs arrange themselves in respect to lengths as represented by the broken line on Diagram I. The base of this curve is long. Its summit coincides with the ordinate of 21 mm. Its interest, of course, lies chiefly in the relationship it bears to the curve of British eggs.

The latter curve is represented by an unbroken line. Its base extends from the ordinate of 18.5 mm. to the ordinate of 25 mm., and its point of greatest altitude is upon the ordinate of 22 mm.

A moment's examination of these curves reveals not only the fact that the American eggs are more variable, *i.e.*, the base of the dotted curve is broader, but it also yields data appropriate to the third and fourth propositions; for it will be observed that the American eggs have undergone a striking reduction in their average length, that is, they show a departure from a previously maintained higher standard, *viz.*, 22 mm. in length, and they are also tending to gather about a new point of equilibrium, *viz.*, 21 mm. in length.

Without commenting upon these observations, which are based upon *absolute* measurements, let us see if the *ratio* of the breadth of the egg to the length, that is, the *shape* of the egg, has also been affected by the withdrawal of natural selection.

The curves on Diagram II are designed to represent the distribution of eggs according to the ratio of their major and minor diameters. When an egg approaches sphericity, the ratio is higher; when it is elongated, the ratio is lower. The more elongated eggs are arranged at the right of the diagram; the short, stumpy ones are arranged at the left. Oval and ellipsoidal eggs naturally occupy positions along the middle ordinates. The broken line, as before, represents the distribution of American eggs, the unbroken line, of British.

On this diagram it will be noted that the American eggs again show a greater amplitude of variation, the base of the dotted curve being nearly one-fifth broader than that of the entire curve. It will also be noted that, appropriate to the third proposition, the American eggs have undergone a striking

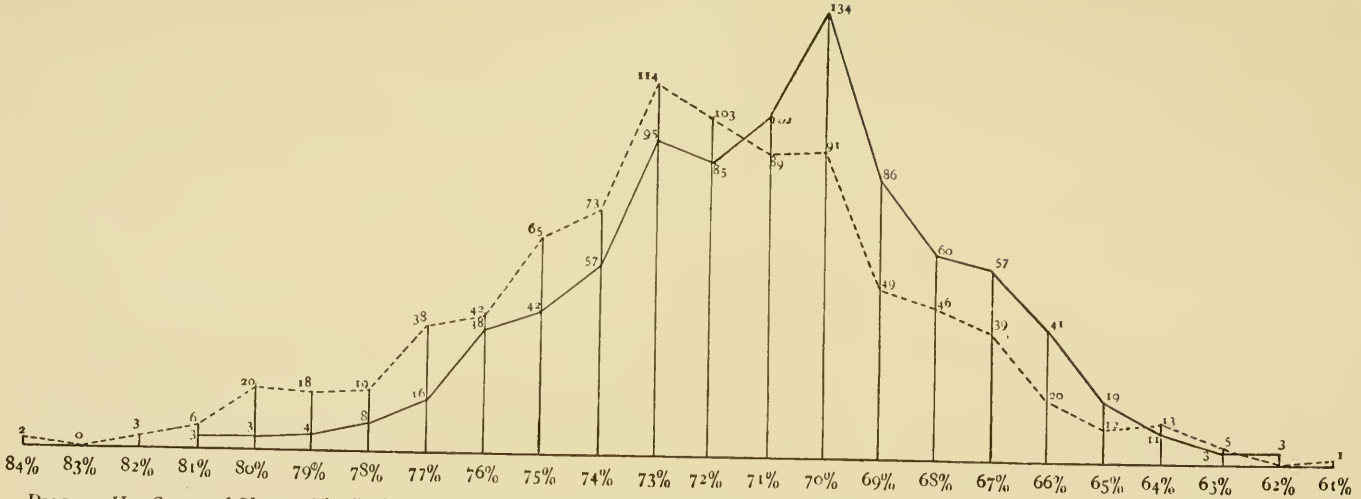

Diagram II. *Curves of Shape.* — The distribution of the American eggs is represented by the broken line; that of the British eggs by the unbroken line. The more nearly spherical eggs are at the left, the more elongated at the right. For example: the figure 84% indicates that the shorter axis of the egg is to the longer as 84 : 100. The number of specimens of each particular shape is represented by the height of the respective ordinate; thus, there are 95 British and 114 American eggs in which the breadth is 73% of the length.

change in shape, as indicated by the ratio of breadth to length; and, appropriate to the fourth proposition, that the American eggs are not indiscriminately distributed, but tend to gather about a mean type. This type is located on or near the ordinate of 73%, and is removed some little distance toward the side of sphericity, and away from the correlative ordinate (70%) of the British specimens.

The second curves, then, bring out in a more emphatic way the same general facts that were shown on the first diagram.

But it is quite evident that the mere ratio of breadth to length is not an adequate index of variation in shape. On this ratio alone, an egg that is conical, or pear-shaped, may not appear in any way different from one that is ellipsoidal or lemon-shaped. I have made several attempts to bring out these extreme variations in some practical arithmetical manner, but have felt each time that the eggs varied far more than the numerical results indicated.

For want of a better method, I finally adopted the following:

Having placed upon each American egg a secret mark, the eggs of both countries were thoroughly mixed together in a single tray. A disinterested person was then requested to select, from the mixture of 1736 eggs, one hundred eggs which appeared to him to present extremes of shape-variation. If eggs from the two countries are equally variable, it is clear that approximately the same number from each would be selected; and, of course, if the American eggs are more variable, more American eggs would be selected. The result of this experiment was most striking, and in harmony with the evidence derived from the comparison of lengths and the ratios of breadth to length. Eighty-one of the selected eggs were American, while only nineteen were English; *over four times as many of the former as of the latter.*

As before mentioned, the colors of both European and American eggs are subject to variation, arising from modifications of the ground color and from the color and distribution of the spots or blotches. Some are of a somber color, much like the eggs of our common song sparrow; others resemble the eggs of the kingbird; and still others have the delicate

ivory white of certain vireos. An attempt was made to arrange the colors in sequence, but after many fruitless efforts the plan of disinterested selection, above mentioned, was adopted.

The British and American eggs were thoroughly mixed together and the request was made that twenty-five eggs which presented the greatest variation toward the kingbird type should be selected first; then twenty-five of the somber type; third, twenty-five of extremely light color; and, fourth, twenty-five anomalous varieties. Some hours were spent in making the selection of one hundred eggs, and with the results indicated on Diagram III, where *b* represents the British eggs and *A* represents the American.

Kingbird Type.	Somber Type.	Light Type.	Anomalous.
b	b	b	b
b	b	b	A
b	b	A	A
b	b	A	A
b	b	A	A
b	b	A	A
b	b	A	A
b	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A
A	A	A	A

Diagram III. — This diagram is designed to illustrate the preponderance of extreme color variation on the part of American eggs. A indicates American, b indicates British eggs.

Of the kingbird type and of the somber type there were over twice as many American as British eggs. There were among the light eggs nearly twelve times as many departures from the

mean of color on the part of the American as on the part of the British eggs, and among the anomalous eggs there were twenty-four times as many American extremes as British. (It may also be of interest to add that the single British egg was the last egg to be selected, that is, it presented the least departure from the mean of the twenty-five anomalous variations.)

Eighty-two of the examples of extreme color-variation were thus found to be American and eighteen British. That so large a proportion of extreme variation in *color* was found among the American eggs is interesting in itself, but a comparison with the relative amount of extreme variation in *shape*, enhances the significance of both results, for not only is the preponderance of variation among American eggs very obvious, but in both cases, in length and in shape, it is almost precisely the same (81 : 19 in the first, 82 : 18 in the second).

Our data, then, whether it be gathered from comparisons of length, ratio of breadth to length, shape, or color, all point in one direction; and, granting that the sparrow since its introduction has been comparatively free from the action of natural selection, we may conclude that the predicted results of Panmixia have been realized.

The collection of a series of facts, for the mere support of some favorite theory, ought not to be the purpose of biological investigation. The relation that the facts may have to other facts and the bearing that they may have upon collateral theories should, at least, be indicated.

The following questions naturally arise:

Apart from the tendency to vary, is the new form, adopted by the American egg, the result of the selection of adaptive adventitious or fortuitous variations, or is it "determinate," the result of the direct action of a new environment? If due to the direct molding influence of a new environment, is the variation *ontogenic*, that is, does it occur anew and repeatedly in each successive generation, in obedience to reiterated environmental demands; or have the directive influences of the mechanism of heredity been so affected that the variation becomes

established as *phylogenic?* Is the mechanism of heredity affected immediately, through the action of the new environment on the germ itself, or mediately, through the influence of ontogenic somatic change?

I think it improbable that the new form adopted by the American egg can be the result of the selection of adaptive fortuitous variations.

Fortuitous variation means *chance*-variation, and, although it is mathematically *possible* for the same particular variation to appear fortuitously in all or nearly all of the American eggs, it is absurd for us to suppose that this has actually happened. We cannot believe that the new form and shape, which are so universally presented by the American species, are variations which have arisen by mere chance. Again, even admitting for the sake of argument that a *chance*-variation has simultaneously appeared in nearly all the American individuals, what have we to show that this variation is adaptive, that it has selective value? Who will say that the shorter egg is a superior egg, or that the more spherical egg is, in the new environment, an improvement on the European type?

In the third place, even admitting the all-sufficiency of natural selection, there has not been sufficient time for the establishment of a new type of egg, that is, for the conclusion of the struggle between "Nature and Nurture." Neo-Darwinians deal with centuries and ages. Forty years can accomplish nothing.

If we again refer to the curves, we shall find other reasons for the belief that the American type of egg is not to be explained by the principle of adaptive fortuity.

Although the American eggs are unquestionably more variable, as is shown by the more elongated base lines, the curves rising to the culminating points of American variation are no less regular than those rising to the culminating points of British variation. This means that the new type is definitely established and that nearly all the eggs tend towards this type. Now, is it likely that mere chance-variation would yield an American curve so nearly parallel to the British curve? If the selection favors those eggs which are located on ordinates 21 and 73 (Diagrams I and II), that is, favors a certain type, why

do other eggs on distinct ordinates and of an entirely different type arrange themselves in an orderly manner?

This brings us to another point. The curves show that the British influence is still felt in America. There are distinct elevations in the American curves as they cross the ordinates of 22 and 70. These elevations, which may represent the conservatism of certain individuals which still retain British instincts, are perhaps of less interest than the elevations on the British curves which lie immediately under the American culminating points. One wonders why ruthless natural selection should have spared these particular individuals.

There has been a *general* reduction in the shape of practically all the eggs since the introduction of the birds into this country, and this reduction has taken place not only in the neighborhood of the new mean, but also at the extremes. Not only has the old culminating point been shifted, but the entire curve has been shifted. The larger eggs have become smaller, the medium eggs have become smaller, the smaller eggs have become smaller; and all the eggs, whether of the ellipsoidal or spheroidal type, have become more nearly spherical.

Concluding, then, that the evidence does not favor the view that the American egg is the result of the action of natural selection upon fortuitous variations, let us examine the alternative, that is, the variations are due to the molding influence of a new environment.

A new environment, offering new food, peculiar climatic conditions, etc., might affect a large number of individuals in certain peculiar and definite ways, and it is evident that the respective curves of variation given in Diagrams I and II are in harmony with such a conception of the march of transformation. It is, indeed, a phenomenon that is seemingly of the nature of a "mutation" (Scott, '94). This view, moreover, is not contrary to the later ideas of Darwin, who distinctly stated that the greatest error which he had committed was in not allowing sufficient weight to the direct action of environment independent of natural selection.

Moreover, if the new environment is directly responsible for the new variations, the question of time is no longer a disturb-

ing factor, and it is perfectly natural that certain less plastic individuals should, through the influence of heredity, continue loyal to the British standard; for the tendencies toward the establishment of a new type are not the result of the selection of the fit nor the elimination of the unfit, but, rather, the result of a direct influence upon all.

The questions remain to be answered: Are the new variations the result of the influence of the environment reiterated in the case of each particular individual, or has the mechanism of heredity been affected so that the American birds are producing new eggs through its directive influence? Has "Buffon's factor" (Osborn, '94), the direct action of environment, produced definite and adaptive variations which are merely "contemporary individual differences" (Cunningham, '93), or are these variations approved and adopted as a part of the constitution of a phyletic series? In brief, is the new variety merely ontogenic, or is it phylogenic?

The maturating as well as the developing ovum must be looked upon as an organism, and "as such must dominate its own development" (Whitman, '94). The ovarian ovum gathers to and about itself certain constituent parts and incorporates them according to its individual peculiarities. As it leaves the ovary, laden with yolk, it gathers about itself the envelopes of albumen, shell-membrane, and shell which it is the function of the oviducal walls to secrete. To assume that the organized ovum has no control, exercises no influence over the development and arrangement of these secondary envelopes, is like assuming that the presence of an ovum in the mammalian uterus exercises no influence upon the uterine walls. But the material submitted to the ovum by the somatic cells is not necessarily always qualitatively and quantitatively the same, and, on the other hand, there is no reason to suppose that any two ova, even of the same parent, have precisely the same peculiarities. The entire bird's egg is the result of the centrifugal influence of the ovum exerted upon the surrounding tissue no less than the centripetal influence of the surrounding tissues exerted upon the ovum; of the keimplasm exerted upon the soma no less than of the soma exerted upon the keimplasm, and, in

dealing with a portion of the resulting structure, *viz.*, the shell, we are dealing perhaps somewhat more directly with the influence of heredity and its vehicle than we would be, if the subject of our discussion were a more distant somatic product, such as a bone or a feather.

The relation of the ovum to the complete egg is practically the same as that of a "caddis-worm," to its "case." The preferred material may be bits of straw, but, in the absence of straw, small pieces of wood may be made to answer. The "worms" in the "cases" of wood are themselves not different from their, perhaps more fortunate, neighbors in straw "cases." It is only when they adopt the wood in preference to the straw that an ontogenic makeshift becomes a phylogenic variation. New building material does not make a new architect.

In America the materials supplied for the developing ovum are different from those supplied in England, and the resulting structure is consequently different. To what extent the new materials have won the favor of the keimplasm cannot be determined by merely allowing American birds to breed again in England, for in England there would be a prejudice in favor of local material, and under the revival of an ancient environment palingenic variation might also deceive. Both English and American birds should be placed in some third locality which combines equally or eliminates the prejudicial environmental conditions of the two countries. Then, and not until then, shall we know to what extent the ontogenic variations in either country have really become phylogenic.

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SECOND LECTURE.

CLEAVAGE AND DIFFERENTIATION.

E. G. CONKLIN.

PHILOSOPHICALLY, the most important problems of biology are those which concern the origin of a new individual, the genesis of a living organism. To the great problem of development has been devoted the earnest thought of philosophers and scientists of every age. The mystery which hangs about the process of progressive and coördinated differentiation by which the egg cell is transformed into the adult never loses its charm nor ceases to be a mystery.

Recent years have witnessed the most remarkable activity in this field, and the views now extant are so numerous, so difficult of concise representation, and have been so frequently discussed that it seems undesirable to dwell upon many of them here. In this lecture I shall present some observations and conclusions derived from a study of the normal development of certain gasteropods and shall attempt to apply these results to some of the current theories of development. Unfortunately, the nature of this material is such as to render direct experiment difficult and in most cases unsatisfactory. Observation, however, is still a valuable method in biology, and it has by no means revealed all that it can, either as to the course or the causes of development. It seems to be assumed in certain quarters that we already know all the important phenomena of normal development and that mere observation is, therefore, a useless and antiquated method. If the time ever comes when every step in the normal development of a single individual is known, the causes of development will not be far to seek. There is no such sharp distinction between observation and

experiment in biology as is sometimes assumed; neither method can arrogate to itself a monopoly of certitude regarding facts or causes. In the solution of the problems of development both observation and experiment are necessary; each has its advantages and its disadvantages and one is no less important than the other.

I. Determinate Cleavage.

Without attempting any final and elaborate definition of so general a term as development, we may for our present purposes say that it is progressive and coördinated differentiation. In all Metazoa and Metaphyta the stages immediately following fertilization are characterized by the cleavage of the egg into a considerable number of cells. The question at once arises as to the relation between cleavage and differentiation. Is differentiation manifested in the cleavage of the egg? Is there any causal relation between cell-formation and differentiation?

There is abundant evidence that there is no *necessary* relation between the two. Many instances of differentiation without cell-formation might be given, *e.g.*, many Protozoa, Protophyta, the spermatozoa and ova of certain animals, intracellular differentiation of many tissue cells, etc. On the other hand, cell-formation may occur without differentiation, *e.g.*, all ordinary divisions of tissue cells and many divisions of embryonic cells. When the two processes are related we may have: (1) cell-formation following the lines of preceding differentiation, *e.g.*, certain cleavages of ctenophores, mollusks, and ascidians; or (2) cell-formation and concomitant differentiation, *e.g.*, many cleavages of turbellarians, nematodes, annelids, and mollusks; or (3) differentiation following the lines of preceding cell-formation, *e.g.*, many cleavages in the eggs of annelids, mollusks and probably many other animals.

In that pioneer work on developmental mechanics (*Unsere Körperform*, 1874) Wilhelm His propounded the doctrine that the organs and parts of an embryo are represented in the early stages of development, perhaps even in the unsegmented egg, by definitely localized germs (*Anlagen*). "The principle, according to which the germinal disk contains the preformed

germs of organs spread out over a flat surface, and conversely, that every point of the germinal disk is found again in a later organ, I call the Principle of Organ-forming Germ-regions (*organbildende Keimbezirke*)." This doctrine has been denied in its totality by some authors, but, although it is still the subject of much controversy, the evidence is accumulating that with certain modifications it is true of a considerable number of animals belonging to several different types. The fact that, under unusual or "abnormal" conditions, regions which would have developed into certain parts develop into others is not a contradiction of the entire principle, though it does limit its causal significance.

Accepting the principle of His as true in certain cases, the relation of cleavage to these "germ regions" might conceivably be of two kinds; cleavage planes might follow the lines of separation between these regions, in which case there would follow a definite form of cleavage, each blastomere being destined to give rise to definite organs or parts of the embryo; or cleavage planes might cut across these regions indiscriminately, in which case an indefinite and inconstant form of cleavage would probably result. Of course, if one does not accept the principle of His, a third alternative is possible and is, in fact, imperative, *viz.*, cleavage is a mere sundering of homogeneous materials and every blastomere at the time of its formation is like every other blastomere.

The first of these alternatives has been presented in what is commonly called the "mosaic theory" of Roux;[1] the second in what might be called the "organization theory" of Whitman;[2] the third in what I venture to call the "homogeneity theory" of Driesch.[3] Disregarding for the present the *causes* of differentiation and viewing merely its *results*, it is probable that each one of these theories is true in certain cases. The study of cell-lineage has shown that in any given species among annelids, mollusks, ascidians, nematodes, and probably among ctenophores, turbellarians, rotifers, and crustacea each blasto-

[1] Roux, W., "Beiträge zur Entwicklungsmechanik des Embryo," Nr. V, 1888.

[2] Whitman, C. O., "The Inadequacy of the Cell-Theory of Development," Biological Lectures, Wood's Holl, 1893.

[3] Driesch, H., "Entwicklungsmechanische Studien," I–VI, *Zeit. wiss. Zool.*, Bde. 53, 55, 1891–93.

mere arises at a definite time, in a definite way, divides into a definite number of cells, each having definite characters, and in the end gives rise to a definite part. In such cases, as Wilson[1] has well said: "The development is a visible mosaic work, not one ideally conceived by a mental projection of the adult characteristics back upon the cleavage stages." Especially in the case of the annelids and mollusks the cleavage is a mosaic work more perfect than anything described by Roux, almost every organ of the larva being represented by a differentiated cell or group of cells before gastrulation is completed.

On the other hand, no such definiteness is known to exist in most cnidaria, echinoderms, and vertebrates, and is, in fact, denied by several excellent observers. In such cases the cleavage is equally inconstant, indefinite, and devoid of morphological significance, whether one conceives with Whitman that the unsegmented egg is mapped out into "germ regions," which are traversed in various directions by the cleavage planes, or whether one holds with Driesch that no such "preorganization" of the egg exists, and that "by cleavage perfectly homogeneous parts are formed capable of any fate."

Obviously the same considerations apply to the axial relations of the cleavage planes and, in case one denies the principle of His, to the polarity of the unsegmented egg. In all cases in which the cleavage has a mosaic character the relation of the egg-axis and of the planes of cleavage to the embryo or adult are perfectly definite and constant, and in many cases in which the cell lineage has not been followed and in which the mosaic character of the cleavage has not been directly recognized the constant relation of the planes of the first and second cleavages to the future planes of symmetry would indicate that the blastomeres bear constant relations to future organs. Whereas in those cases in which the egg-axis or the position of the early cleavage planes is inconstant the individual blastomeres can bear no constant relation to adult structures.

Confusion has already arisen through a failure to distinguish these two types of cleavage; much of the recent experimental

[1] Wilson, E. B., "The Mosaic Theory of Development," Biological Lectures, Wood's Holl, 1893.

work in embryology has been done upon forms in which the cleavage is not known to be constant, and general conclusions have been drawn which are plainly inapplicable to forms in which the cleavage is constant and definite. Although it is probable that there are forms which are intermediate between those which show extreme constancy and those which manifest extreme inconstancy of cleavage, yet the existence of two such *types* of cleavage must be recognized, and, as it is desirable to clearly distinguish between them, I propose to designate these types by the terms *determinate* and *indeterminate*. This is to be understood as applying only to the cleavage, for in its main features and results the development of all animals is determinate, that is, predictable. Even in cnidaria, echinoderms, and vertebrates the *general form* of the cleavage is constant and there appears successively a blastula, gastrula, larva, and adult of determinate form and character. The question is whether such determinism, which appears sooner or later in all cases, applies to the individual blastomeres of the cleavage stages.

Determinate cleavage is both *constant and differential*. It is more than constant, for in constant cleavage every blastomere might be like every other (Driesch); it is more than differential, for differential cleavage might be of such a sort that it is never twice alike (Whitman). It is the same as *mosaic cleavage*, but this name is not used because of the implication which it involves as to the cause of differentiation; determinate cleavage does not necessarily imply "self-differentiation" of blastomeres, which is such an important part of Roux's "mosaic theory." Cleavage is indeterminate when it is either inconstant or non-differential or both.

Among certain gasteropods [1] which I have studied the cleavage is of a highly determinate character as regards both the history and destiny of individual blastomeres and the relation of the cleavage planes and egg-axis to the future planes of symmetry. The chief axis of the ovum is established before fertilization, probably in the ovary, and it determines the

[1] Four species of Crepidula, Urosalpinx, Sycotypus, Fulgur, Tritia, Illyonassa, and Bulla.

gastrular axis and the cephalic and oral poles of the larva. In many cases the antero-posterior axis is marked out by the inequality of the first cleavage, and this is preceded by the eccentricity of the nuclear spindle, which in turn must be the result of the structure of the unsegmented egg. The direction of the first cleavage in Crepidula and probably in the other cases mentioned is always dexiotropic, that is, of such a character that the nuclei and protoplasmic areas of the two resulting cells rotate in a clockwise direction at the close of the cleavage (Fig. 1). This character must also be predetermined in the unsegmented egg. It is the first of a long series

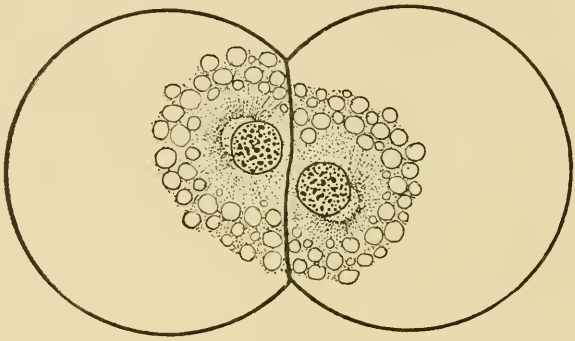

FIG. 1. — Crepidula, 2-cell stage; showing dexiotropic rotation of nuclei asters and cytoplasm at the close of the first cleavage.

of "spiral cleavages" (Figs. 2, 3, 4) which are oblique alternately to the right and to the left, each of which, except the first, finds the cause of its direction in that of the preceding cleavage. The direction of these cleavages stands in the most intimate relation to the origin of the mesoblastic pole cells, the appearance of bilateral symmetry, and the direction of the asymmetry of the adult. In all cases in which the first cleavage is dexiotropic the pole cells of the mesoblast arise from the left posterior macromere by laeotropic division (Fig. 4); where the first cleavage is laeotropic (as in some sinistral gasteropods) they arise from the right posterior macromere by dexiotropic division. In Crepidula bilateral symmetry appears in different directions in the ectoblast, mesoblast, and entoblast, and by a subsequent laeotropic rotation, which is dependent

upon the direction of certain cleavages and ultimately upon the first cleavage, these diverse planes of symmetry come to coincide in a common plane. The direction of the asymmetry of the adult Crepidula is also referable to the time and direction of certain cleavages (of the fifth quartette) which are explained in part by the direction of preceding divisions and finally by the direction of the first cleavage; whereas in certain sinistral gasteropods, as Crampton [1] and Kofoid [2] have shown, the direction of all the cleavages is reversed.

All of these important and determinate characters are directly

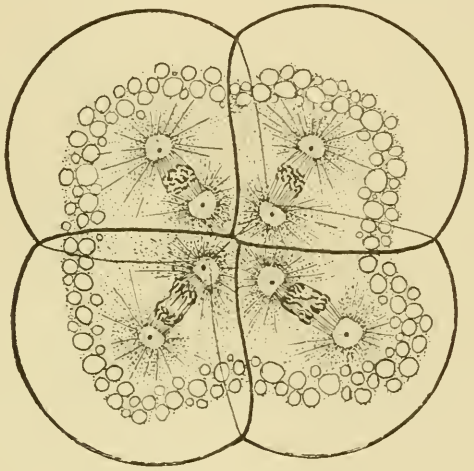

FIG. 2. — Crepidula, third cleavage; early indications of a dexiotropic rotation.

referable to certain peculiarities of the unsegmented egg, and although it is not possible to trace all determinate characters to this early stage, yet it is highly probable that many others are due to the same cause. How suggestive in this connection are the observations of Blochmann [3] upon the *Urvelarzellen* of Neritina; these cells contain a mass of coarse granules which can be traced back through previous generations of cells until

[1] Crampton, H. E., "Reversal of Cleavage in a Sinistral Gasteropod," Ann. New York Acad. Sciences, VIII, 1894.

[2] Kofoid, C. A., "On Some Laws of Cleavage in Limax," Proc. Am. Acad. Arts and Sciences, XXIX, 1894.

[3] Blochmann, F., "Ueber die Entwicklung der Neritina fluviatilis," *Zeit. wiss. Zool.*, Bd. 36, 1881.

they appear in the protoplasm of the unsegmented egg itself on each side of the animal pole. Likewise the observations of Driesch and Morgan [1] on ctenophore eggs indicate what a high degree of organization the unsegmented egg may reach. And while it is conceivable that this high degree of organization of the egg may not lead to a highly determinate form of cleavage, yet it is to be observed that in all the cases named this does happen.

All the earlier cleavages in Crepidula are spiral, that is, radially symmetrical, and this radial symmetry extends not only to the

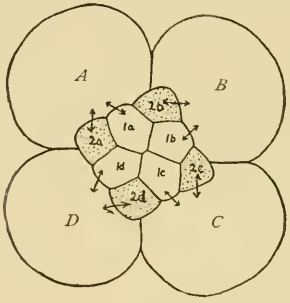

FIG. 3.

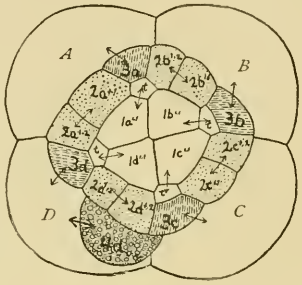

FIG. 4.

FIG. 3. — Crepidula, 12-cell stage; four macromeres and eight micromeres.

FIG. 4. — Crepidula, twenty-five cells; t_1 trochoblasts. In these and some of the following figures the macromeres and first quartette are unshaded; the second quartette is stippled; the third quartette is shaded with lines; and the fourth quartette (4d) with dots and circles. The direction of the various cleavages is shown by means of arrows.

direction and time or rate of division, but also to the size, the position, and the histological character of the resulting blastomeres. The result is a number of radial structures such as the four trochoblasts (Fig. 4, t), the four arms of the ectoblastic cross (Fig. 5 *et seq.*), and the four rosette series of cells (Figs. 10, 12), some of which give rise to certain radial structures of the larva. Not a single bilateral cleavage appears up to the 44-cell stage, and radial cleavages generally prevail throughout the egg until a much later period. In all cases bilateral cleavages first appear in certain cells on the posterior side of the egg and in processes which lead to the elongation of the body along the posterior axis. This bilater-

[1] Driesch und Morgan, "Zur Analysis der ersten Entwicklungsstadien des Ctenophoreneies," *Arch. für Entwicklungsmechanik*, Bd. 2, 1895.

ality of the cleavage is directly and causally related to the bilaterality of the larva and the adult, though in some cases extensive rotations of cells and even of entire layers are necessary in order to bring blastomeres and planes of symmetry into their proper positions.

Apart from qualitative cell divisions, which are undoubtedly an important factor in differentiation, differential cleavages are the result of differences in the time and direction of division and in the size of the daughter cells. If divisions were always synchronous, alternating, and equal almost all the visible features of differential cleavage would disappear; it is in the constancy of certain peculiarities in the rate and direction of division and in the size of resulting cells that determinate cleavage is chiefly manifest.

Among the gasteropods mentioned above, the rate of growth and division of certain cells is highly peculiar, and in general this cannot be explained by the presence of yolk or by other extrinsic (that is, non-protoplasmic) causes. Adjacent and apparently homogeneous cells may behave in the most remarkably unlike ways in this regard. For example, the trochoblasts are at the time of their formation the smallest cells in the entire egg (Fig. 4); they grow rapidly, but divide rarely, and are characterized by having clear, non-granular protoplasm. On the other hand, the apical cells which gave rise to the trochoblasts are composed of granular protoplasm, and, although they grow scarcely more than the trochoblasts, they divide repeatedly, each of them giving rise at the stage shown in Fig. 10 to twelve cells, the total volume of which scarcely exceeds that of a single trochoblast. Many other illustrations of this same fact might be given.

In the departure of certain cells from the rule of alternating cleavage, or Sachs' law of rectangular intersection, we have another factor of differentiation and a marked feature of determinate cleavage. This is beautifully shown among the gasteropods named in the transition from radial to bilateral cleavages; in such cases the direction of division is reversed usually in one cell of a quartette (Fig 6). It is also shown in all cases of teloblastic growth, of which there are many at the posterior pole

of the egg, where repeated divisions are in the same direction, and apparently in the shortest diameter of the protoplasm and in the line of greatest resistance. It appears also in the formation of certain definite structures, such as the ectoblastic cross, where the direction of a certain division is reversed in each arm. Upon this reversal depends the existence of the cross as such, and presumably of certain structures to which it gives rise.

Another remarkable instance of determinate cleavage is found in the unequal division of cells. Such unequal division constantly occurs in the formation of certain cells and is one of the most striking features of determinate cleavage. As has been said, the first cleavage may be unequal, though in most species the first and second cleavages divide the egg into nearly equal cells. In the formation of the three quartettes of ectomeres, however, the divisions are usually very unequal (Figs. 2, 3, 4), while in the formation of the fourth and fifth quartettes divisions are again more nearly equal. I have already called attention to the very small size of the trochoblasts when first

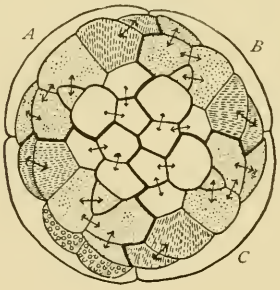

FIG. 5.

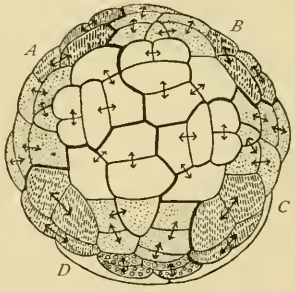

FIG. 6.

FIG. 5. — Crepidula, 42-cell stage. Shading as in Figs. 3, 4. The cross (shown in strong outline) lies in the position in which it was first formed. The heavy, radiating lines separate the cells of the different quadrants.

FIG. 6. — Crepidula, 60-cell stage. The whole of the ectoblast has rotated to the left, due to the rotation of the fourth-quartette cells. The middle cells in three arms of the cross have divided transversely. The third-quartette cells of the posterior quadrants have divided bilaterally.

formed; another illustration is found in the tip cells of the cross (Fig. 5). In fact, no phenomenon is more common in determinate cleavage than the unequal division of apparently

homogeneous cells; such divisions are extremely constant and in many cases are visibly differential. Even in the case of the echinoderm egg it has been shown that four micromeres are constantly formed at one pole of the egg, and in this respect, at least, the cleavage here is determinate, for although Driesch has shown that a normal larva develops from a sea-urchin egg from which the micromeres have been removed, this no more indicates, as Morgan[1] assumes, that these micromeres are undifferentiated and that the cleavage is, therefore, indeterminate than the fact that a hydra is able to complete itself and form a normal hydra after its tentacles have been removed indicates that these tentacles are undifferentiated.

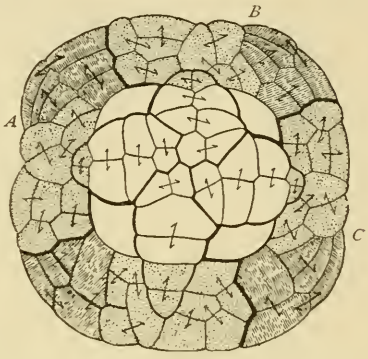

FIG. 7. — Crepidula, 109-cell stage (ninety-two ectoblast cells). Shading and heavy lines as in preceding figures. The egg is represented as if all the ectoblast cells could be seen from the apical pole, though actually many of the peripheral cells lie far down on the sides, or even on the ventral face of the egg.

The one most striking feature of determinate cleavage is the constancy with which certain blastomeres give rise to certain organs, the invariable segregation of an entire region, layer, or organ into a single cell or particular group of cells. In all the gasteropods mentioned above the ectoderm comes from three quartettes of cells, each of which occupies relatively the same position and gives rise to the same organs (Fig. 4). The mesoderm comes from the posterior cell of the fourth quartette. All the other cells are entodermal, and, although they show certain variations in size and position in different genera, owing to variations in the amount and distribution of yolk, they are always constant for the same species. The four apical cells give rise to an apical sense organ (see Figs. 3–10), the trochoblasts and tip cells of the cross form the first velar row, the anterior arm of the cross forms the anterior cell plate,

[1] Morgan, T. H., "A Study of a Variation in Cleavages," *Arch. für Entwicklungsmechanik*, Bd. 2. Hft. 1.

the posterior arm the posterior cell plate, the anterior rosette series gives rise (at least in part) to the cerebral ganglia, the shell gland and growing point come from the posterior member of the second quartette (2d), the paired mesoblast bands and the distal end of the intestine from the posterior member of the fourth quartette (4d), the roof of the archenteron from the remains of the four primary macromeres, its sides and floor from the fifth and fourth quartettes respectively; in fact, so many cells may be traced through to definite organs or parts that one is justified in concluding that under normal conditions every one of the earlier blastomeres gives rise to a particular part. *The constancy with which differentiated cells give rise to differentiated layers, regions, and organs is the most fundamental fact of determinate cleavage.*

What is the cause of determinate cleavage?

Such widespread, precise, and constant phenomena cannot, of course, be due to chance; nor are they the result of universally acting mechanical causes, such as gravity or surface tension. Certain indeterminate features of cleavage may be directly referred to extrinsic factors or mechanical conditions; *e.g.*, the rotation of cells into the furrows between blastomeres is probably referable to the principle of surface tension or mutual pressure, the contour of cells is frequently the result of intercellular pressure, the alternation of successive cleavages is an expression of the principle of rectangular intersection of cleavage planes, and this in turn may be due to the fact that the nuclear spindle usually lies in the direction of the greatest mass of protoplasm, and hence in the direction of least resistance. These features, however, are neither constant nor differential. So far as the principle of surface tension is concerned cells might rotate to the right or to the left indiscriminately, yet in determinate cleavage the direction of rotation is perfectly constant. So, also, it frequently happens that successive cleavages do not alternate in direction, and in such cases the nuclear spindles often appear to lie in the direction of greatest pressure. In general, the direction of teloblastic and non-alternating cleavages can be referred only to peculiarities in the protoplasmic structure of the cells, and, as I have pointed

out, the constancy with which the first cleavage is dexiotropic is evidence of a constant peculiarity of the protoplasm of the unsegmented egg. Likewise the factors which determine the varying rate of division of certain blastomeres are generally intrinsic and protoplasmic rather than extrinsic; on no other basis can one explain the great difference in the rate of divi-

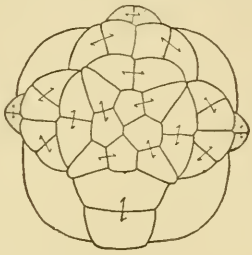

FIG. 8.

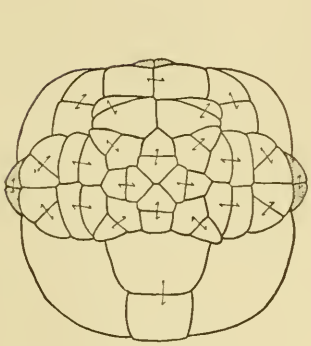

FIG. 9.

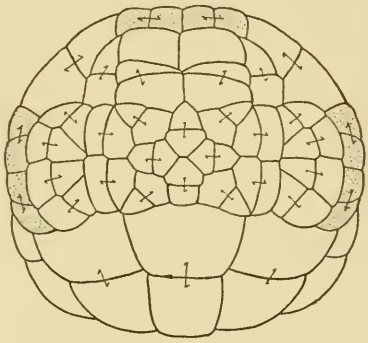

FIG. 10.

FIGS. 8–10. — First quartette in Crepidula, showing the later history of the cross and trochoblasts.

sion of contiguous cells. It is the same with that other marked character of determinate cleavage, — unequal divisions. In all cases in which unequal cleavage is not forced upon a cell from without, *e.g.*, by unequal pressure, it must be regarded as an expression of a difference in the material substance of the dividing cell. In the separation of the micromeres from the macromeres there is a most marked material differentiation, one cell being purely protoplasmic, the other containing all the yolk. Even in cases of unequal cleavage in which the cell substance is apparently homogeneous, as, for example, in the

formation of the trochoblasts and of the basal and tip cells in the arms of the cross, the initial eccentricity of the nuclear spindle indicates that here also there must be some difference of material substance within the cell, though not directly visible. Sachs[1] has well said, "The external form as well as the internal structure of any body are the necessary expression of its material constitution. Difference in form always indicates difference of material substance." That the cause of unequal cleavage is more complex than the mere mechanical displacement of the nuclear spindle is proven by the fact that the first two divisions of the egg are frequently equal, though the polar differentiation of the protoplasm and yolk is as marked as in later divisions which are very unequal.

What and how many factors enter into the complex of causes which produce even such simple phenomena as non-alternating, non-rhythmical, and unequal cleavages it is at present impossible to say; however, the prospective significance, the "purposefulness," of such cleavages is often very apparent. Lillie[2] has pointed out the fact that unequal cleavages in Unio stand in direct relation to the size of the parts arising from the blastomeres. With the following slight modification this principle is applicable to all the gasteropods which I have studied, *viz.*, the initial size of the blastomere stands in direct relation to the size and the time of formation of the part to which it gives rise. In fact, this is but a partial expression of a much more general truth, *viz.*, that all differential cleavages, whether non-alternating, non-rhythmical, or unequal, are directly and causally related to the uses to which these cells are put, — in short, to the general differentiation of the organism.

Other attempts have been made to explain the definite relation between blastomeres and organs than the one here given, *viz.*, that the differentiation of the blastomere stands in direct relation to the differentiation of the parts and that the former is the result of differences in the material constitution of the cells. Hertwig[3] ascribes the fact that organs may be traced

[1] Sachs, J. v., "Physiology of Plants," Lecture XLIII, 1882.

[2] Lillie, F. R., "The Embryology of the Unionidae," *Journal of Morphology*, X, 1895.

[3] Hertwig, O., "Urmund und Spina-bifida," *Arch. für mik. Anat.*, Bd. 39, 1892.

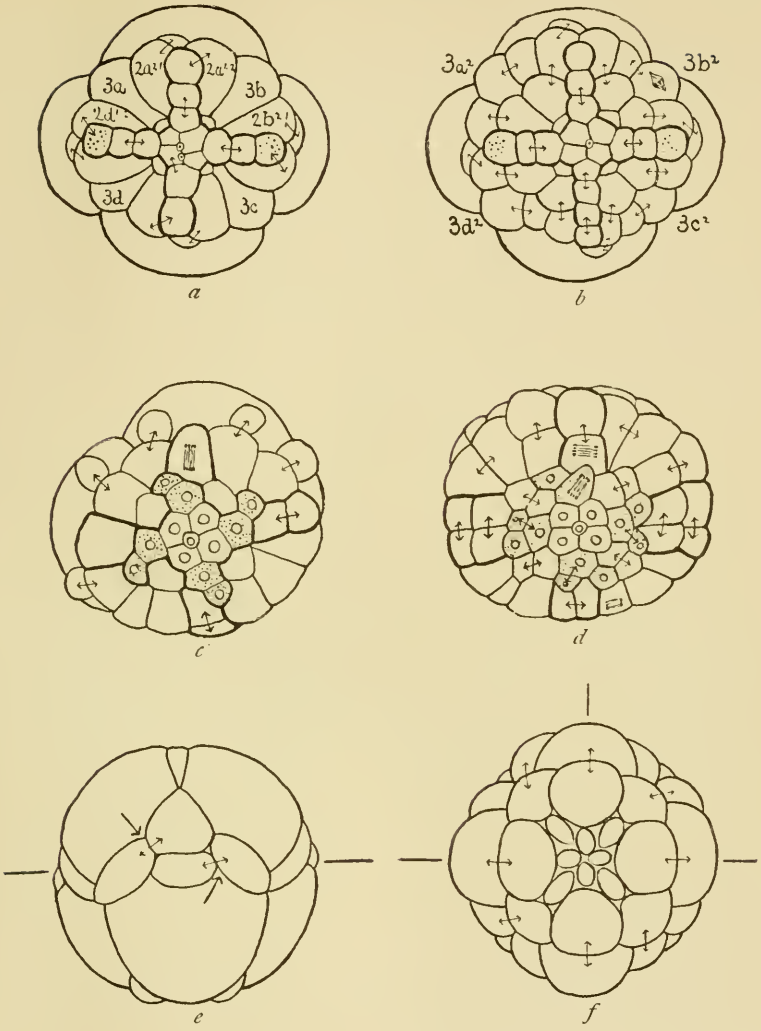

FIG. 11.—The cross in Neritina, Umbrella, and Chiton.—*a*, Neritina: three cells in each arm except the posterior; the granular tip cells of the transverse arms are the "Urvelarzellen." (Blochmann's Fig. 53.)—*b*, Neritina: four cells in the posterior arm, three in each of the others. The probable origin of the outer belt cells is indicated by arrows, and the designation of the cells in this and in the preceding figure are given as in Crepidula. (Blochmann's Fig. 56.)—*c*, Umbrella: the arms of the cross are stippled; Heymons' so-called "cross" is shown in heavy outline. (Heymons' Fig. 14.)—*d*, Umbrella: stippling and outlines as in *c*. The basal cells in the arms of the cross have divided laeotropically, the trochoblasts bilaterally. (Heymons' Fig. 20.)—*e*, Chiton: lateral view of the 32-cell stage. The small cells around the equator of the egg correspond in origin and position to the *trochoblasts* and the *tip* cells of the gasteropod; they should form the prototroch if they have the same destiny in the two cases. (Metcalf's Fig. XIV.)—*f*, Chiton: apical view of the 48-cell stage, showing the *cross*, the *rosette*, and the *trochoblasts*. (Metcalf's Fig. XXIV.)

back to certain blastomeres to the "continuity of development." "In consequence of the continuity of development," he says, "every older cell group must arise from a preceding younger cell group and so finally definite parts of the body from definite segment cells." A truer conclusion would be: and so finally definite parts of the body from any cell you please. Continuity of development no more explains the fact that the first cleavage is dexiotropic, that the ectoderm is segregated in three quartettes of cells, that the mesoderm comes from a definite cell of the fourth quartette, that certain cells always give rise to certain organs, than gravitation does. Likewise the "interaction of cells" which Hertwig and Driesch have invoked to explain so many features of differentiation is in this case an insufficient explanation. How can cellular interaction explain the fact that from the time of its formation a certain blastomere, *e.g.*, the *Urvelarzelle* of Neritina, is peculiar in size and histological character or that it grows rapidly and divides rarely, whereas an adjoining cell, the apical, grows slowly and divides rapidly? If it is meant that differentiation is the result of the interaction of different material substances of the *protoplasm* which are more or less definitely localized, then there can, of course, be no objection to this view.

These are but a few of the many striking features of determinate cleavage which are not at present explicable by known mechanical causes. In the main one is compelled to refer determinism in development, whether it be in cleavage, the formation of organs, or the reproduction of specific and individual characters, to intrinsic causes, that is, to the structure of the germinal protoplasm, without for the present being able to explain *how* such protoplasmic structure is able to produce such predictable results.

Even Driesch, who represented very different ideas in his earlier writings, has said in one of his later papers:[1] "The facts make it necessary to suppose that there exists in the plasma-structure of every fertilized egg of a bilateral animal a polar-bilateral direction of its particles. . . . In addition there

[1] Driesch, H., "Betrachtungen über die Organisation des Eies und ihre Genese," *Arch. für Entwicklungsmechanik*, Bd. 4, 1896.

are present in many eggs different non-miscible substances which may predispose cells during cleavage to essentially different prospective values (micromeres and macromeres), and finally definite substances are definitely localized in the eggs of many

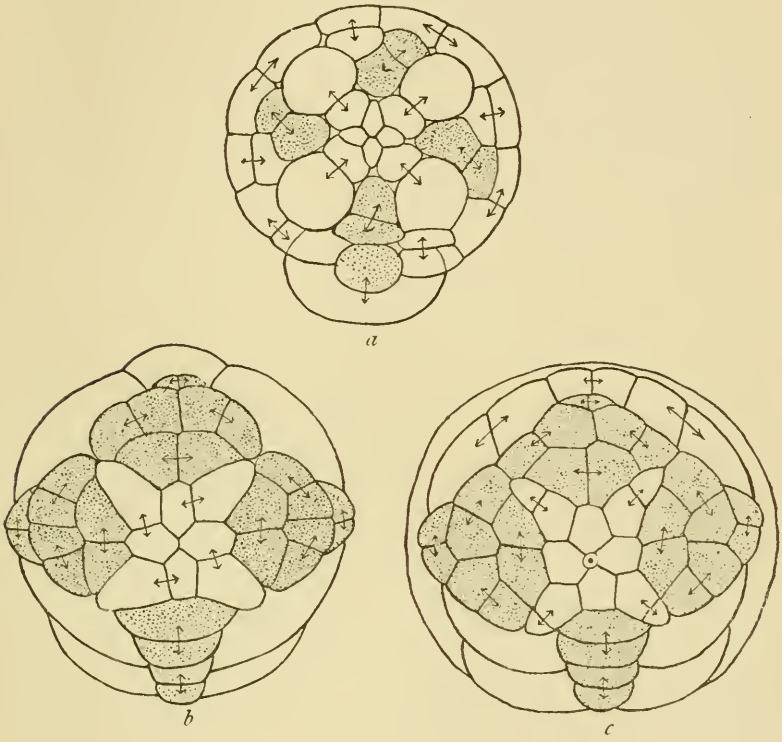

FIG. 12. — The cross in Nereis and Crepidula. — *a*, Nereis : the stippled cells are the *intermediate girdle cells* (molluscan cross) excepting the posterior one (x^3) which corresponds to the "tip cell" in the gasteropod. The trochoblasts lie at the margin of the egg. (Wilson's Diagram H. B.) — *b*, Crepidula : cross cells (intermediate girdle cells of Nereis) are stippled. Apical and rosette cells unshaded as in *a*. Trochoblasts around margin. — *c*, Crepidula : shading as in *b*; rosette cells and anterior trochoblasts divided.

animals which permit one to recognize necessary relations to certain early, firmly established organs. . . . In certain cases axial relations may be stamped upon eggs through the action of external factors; in the majority of cases, however, especially in eggs with complicated structure, this is not the case; the organization is here performed in the unfertilized egg, that is,

it has arisen in the course of ontogeny (oögenesis) as a typical differentiation, at a typical place of the entire germ, through typical formative internal stimuli" (p. 99). After such sweeping concessions from the most vigorous opponent of the principle of His and of the mosaic theory of Roux we may now consider determinate cleavage, at least in certain cases, as no longer a matter of controversy. In conclusion one may say of all determinate cleavage that *the reason that a certain blastomere arises in a certain way, passes through a definite developmental history, and in the end gives rise to a definite part is at bottom the same reason that the egg of a given animal passes through a definite history and gives rise to a definite organism.*

II. Cell Homology.

In the search for the earliest appearing homologies in the development of organisms embryologists have generally been content to stop with the germinal layers. This has been chiefly due to the fact that there is such great diversity in the pregastrular stages of most animals that they cannot be brought into any single system. There are various types of cleavage, such as the meroblastic and holoblastic, the alecithal, telolecithal, and centrolecithal, the radial, bilateral, and asymmetrical, the determinate and indeterminate, and, while it is possible to hypothetically connect them, it is not possible at present to compare the blastomeres of one type with those of any other. If any similarity ever existed between the blastomeres of an arthropod and of an annelid or of a cephalopod and of a gasteropod the alteration of the type of cleavage has completely destroyed it. Any attempt to establish cell homologies must be limited not only to a single type, but also to determinate, that is, constant and differential cleavage. In addition, any detailed comparison of the cleavage stages of various animals demands an accurate knowledge of the cell-origin of various parts and organs, and this is unfortunately lacking except in a few cases.

If, within the limits indicated, we compare the cleavage of one species with that of other related species or genera we find many identical characters running through all of them. Among

the gasteropods these resemblances of the cleavage stages are marvelously accurate and complete; even among forms showing the greatest diversity in the size and structure of the egg, in the method of gastrulation and in the adult these resemblances are minute and long continued. Among the most diverse types of prosobranchs, opisthobranchs, and pulmonates very many blastomeres are identical in method of origin, relative position, and ultimate destiny. In fact, so far as now known, all gasteropods have not only the same type of cleavage, but all manifest the most fundamental similarity in the developmental history of individual blastomeres.

The amount and distribution of yolk has little influence on these resemblances. The egg of Crepidula adunca is 27 times as large as that of C. plana, and yet every cleavage is identically the same up to the 52-cell stage. The egg of Fulgur is 140 times as large as that of C. plana, and yet the early cleavages and the ultimate fate of the blastomeres is almost exactly the same in the two cases.

In the distribution of the yolk the most diverse conditions are found associated with the most fundamental resemblances in the origin and history of the blastomeres. In many eggs the yolk is equally distributed to the first four cells, *e.g.*, four species of Crepidula, Neritina, Planorbis, Sycotypus, Fulgur, and Bulla. In others it is chiefly aggregated in one, two, or three of the macromeres, *e.g.*, Urosalpinx, Illyonassa, Tritia, Aplysia, Umbrella, etc. In general, if one macromere is larger than another, it is the posterior one among prosobranchs and the anterior one among opisthobranchs. Although this unequal distribution of yolk makes marked changes in the form of the embryo, it scarcely influences in a single respect the typical formation and development of blastomeres.

In one respect there seems to be a notable difference between forms otherwise remarkably alike. In a large number of gasteropods (Neritina, Planorbis, Vermetus, Aplysia, Urosalpinx, Tritia, Nassa, Illyonassa, etc.) the first and second cleavage planes are oblique to the median plane of the embryo, whereas in another series of forms (Crepidula, Umbrella, Sycotypus, Fulgur, etc.) the first cleavage is approximately transverse to

the median plane and the second coincides with it. The axial relations of the first two cleavages being different in these cases, it seems that the first four cells must give rise to different organs in the two classes named. However, a careful examination shows that in all these cases the ectomeres and mesomeres rotate so as to occupy relatively the same positions and ultimately give rise to the same parts (Fig. 6); the position of the entomeres alone is different. It seems to me very probable, considering the extensive shifting which the entomeres undergo in late stages, that even the axial differences of these cells may ultimately disappear, but even if they do not it is certainly a matter of secondary importance that a few cells forming a tubular internal canal should occupy slightly different axial relations as compared with the fact that hundreds of cells occupy relatively the same positions and give rise to the same organs. The entomeres have undergone great modifications owing to the acquisition and loss of yolk and its varying distribution to the different macromeres, and it would not be surprising if they have also shifted their axial relations in some cases. On the whole, this apparent difference in the axial relations of the first two cleavages affords an unexpected confirmation of the fundamental likeness of all gasteropod cleavage.

These important resemblances of cleavage stages are not limited to the gasteropods. Wilson [1] has pointed out a number of remarkable similarities in the cleavage of polyclades, annelids, and gasteropods; Lillie [2] has shown that the lamellibranch cleavage is essentially like that of the gasteropods and annelids; and Heath [3] has recently discovered that the cleavage of Chiton resembles in the most wonderful manner the cleavage of all the groups just named.

"Wilson emphasizes the following important resemblances between the early cleavage stages of the annelid, the polyclade, and the gasteropod: (1) the *number and direction of the cleavages* is the same in all three up to the 28-cell stage; (2) in

[1] Wilson, E. B., "The Cell Lineage of Nereis," *Journal of Morphology*, VI, 1892.

[2] Lillie, F. R. "The Embryology of the Unionidae," *Journal of Morphology*, X, 1895.

[3] Heath's work is not yet published.

general, the cells formed are *similar in position and size, viz.*, there are four macromeres, three quartettes of micromeres, and the first quartette is surrounded by a belt composed of the second and third quartettes. The first quartette undergoes three spiral divisions in alternate directions, and the second quartette divides once. Here the resemblance with the polyclade ceases, though the annelid and gasteropod go one step further in these likenesses, *viz.*, (3) the *three quartettes of micromeres are ectomeres* in the annelid and gasteropod, and (4) in both these groups *the mesoblast is formed from the cell 4d*, which gives rise to paired mesoblastic bands.

"Beyond this point Wilson believed that the annelid diverged from the gasteropod. He supposed that the 'cross' in the two was wholly different both in origin, position, and destiny, and that the velum had a wholly different origin from the annelidan prototroch.

"Lillie has extended all the above-mentioned resemblances between annelids and gasteropods to the lamellibranchs, and in addition has discovered the following: (5) the *first somatoblast* (2*d*), which gives rise to the ectoderm of the trunk, has exactly the same origin and position and a similar history in the annelid and lamellibranch; (6) it gives rise to a *growing point* and a *ventral plate* in all respects essentially like those of the annelids. Lillie shows good reason for believing that in other mollusks the posterior growing point is derived from these cells.

"To this list of resemblances between the annelid and the mollusk, which I can confirm in the case of the gasteropod, I have been able to add the following: (7) the *rosette series* of the gasteropod is exactly like the *cross* of the annelid in origin, position, and probably in destiny. The *intermediate girdle cells* of the annelid are like the *cross* of the gasteropod in origin, position, and destiny (at least in part) (Fig. 12). The differences, therefore, between the annelidan and molluscan cross which Wilson emphasizes are not real ones; (8) the *trochoblasts* of the annelids and gasteropods are precisely similar in origin and destiny (at least in part) (Figs. 10, 12). In some annelids (Amphitrite, Clymenella, Arenicola), the prototroch is completed by cells of the same origin as in Crepidula and Neri-

tina. The differences which Wilson points out between these two structures do not, therefore, exist. In both annelids and mollusks the prototroch lies at the boundary between the first quartette on one side and the second and third on the other. In both there is found a preoral, an adoral, and a post-oral band of cilia; (9) in the gasteropod the apical cells give rise to an *apical sense organ* such as is found in many annelid trochophores; (10) the *supra-oesophageal ganglia and commissure* apparently arise from the same group of cells in annelids and gasteropods; (11) the *fourth quartette* in annelids and gasteropods contains mesoblast in quadrant D, but is purely entoblastic in quadrants A, B, and C; (12) a *fifth quartette* is formed in gasteropods and some annelids (Amphitrite, etc.), and consists of entoblast only; (13) in the gasteropod *larval mesoblast* arises from the same group of ectoblast cells as in Unio, differing, however, in this regard, that it is found in quadrants A, B, and C, whereas in Unio it is found in quadrant A only; (14) to this list of accurate resemblances in the cleavage cells may be added the fact that *among annelids and mollusks the axial relations of all the blastomeres* (*except possibly the four macromeres*) *are the same.*

"What a wonderful parallel is this between animals so unlike in their end stages! How can such resemblances be explained? Are they merely the result of such mechanical principles as surface tension, alternation of cleavage, etc., or do they have some common cause in the fundamental structure of the protoplasm itself? Driesch answers: 'The striking similarity between the types of cleavage of polyclades, gasteropods, and annelids does not appear startling; it is easy to understand this, since cleavage is of no systematic worth.' To this, I think, it need only be said in reply that if these minute and long-continued resemblances are of no systematic worth, and are merely the result of extrinsic causes, as is implied, then there are no resemblances between either embryos or adults that may not be so explained. And, conversely, these resemblances in cleavage, however they have been produced, stand upon the same basis with adult homologies."[1]

[1] "Embryology of Crepidula," *Journal of Morphology*, XIII, No. 1.

The cause of such resemblances, like the cause of determinate cleavage and of the constancy of specific characters, must be found in protoplasmic structure, and I cannot escape the conviction that these likenesses belong to the same category with the fundamental resemblances between gastrulae, larvae, and adults. Whatever criterion of homology one may adopt — whether similarity of origin, position, history, or destiny, or all of these combined — certain of these resemblances in cleavage bear all the marks of true homologies.

It is freely granted once for all that even in the limited form in which it is here maintained there are serious difficulties in the way of the doctrine of cell homology. The most important of these difficulties are the following: (1) Related animals do not always have similar cleavage, *e.g.*, cephalopods and other mollusks; triclades, and polyclades. Even within a single order there may be important differences; thus the cleavage is markedly radial in Discocoelis and as markedly bilateral in Polychaerus. Among the Crustacea there are four types of cleavage (see Korschelt und Heider, *Lehrbuch der Entwicklungsgeschichte*): (*a*) total and equal, (*b*) total and later superficial, (*c*) purely superficial, (*d*) discoidal. Finally, contradictions reach a climax among the Daphnidae, where the summer and winter eggs of the same species may belong to wholly different types of cleavage, as Watasé [1] has pointed out. No cell homology is recognizable in such cases, and possibly none exists. (2) Similar larval or adult parts may arise through very different types of cleavage; *e.g.*, the primitive streak of sauropsida and mammalia, the adult structures of amphioxus as compared with most other vertebrates, the shell gland of gasteropods and cephalopods. Such cases show that adult homologies are not necessarily dependent upon cell homologies. (3) Similarities in cleavage may not lead to similarities in subsequent stages, *e.g.*, the cleavage of certain polyclades is closely like that of annelids and mollusks, and yet the cells which are mesomeres in one case are ectomeres in the other. However, the discovery of larval mesenchyme in Unio and Crepidula has lessened the difference in this regard, and it is possible that a further

[1] Watasé, S., "Studies on Cephalopods," *Journal of Morphology*, IV, 1891.

comparison would bring these two groups into still closer agreement. (4) Finally, experiment has shown that the form of determinate cleavage, which alone is under consideration, may be modified in certain regards without materially modifying the results of development. It must not be supposed, however, that such experiments destroy belief in either determinate cleavage or cell homology. That certain forms of cleavage are determinate, *i.e.*, under normal or usual conditions constant and differential, is a visible fact; that certain cells in related animals normally give rise to the same parts is also a fact which cannot be denied. Experiment shows that this normal condition may be modified; it does not prove its non-existence. Even if it should be shown that the apical organ might be formed in the absence of the apical cells or that the mesoblast might appear after the removal of the cell 4d — and be it observed such a thing has never been proved — the case would not be fundamentally different from the regeneration of adult parts after their complete loss, and the doctrine of homology would no more be destroyed in the one case than in the other. On the whole, experiments on determinate cleavage (*e.g.*, Driesch and Morgan[1] on the ctenophore and Crampton[2] on the gasteropod) lend support to the doctrine of cell homology.

A consideration of these difficulties, especially of the first and second, shows how futile is any attempt to establish the *universal* homology of blastomeres, and it indicates, as Wilson has pointed out in his lecture on the "Embryological Criterion of Homology," that embryological likeness or unlikeness is not in itself a sufficient test of homology; it indicates, as do many other considerations, that the early stages of development have undergone profound modifications in the course of evolution, but it does not prove that these early stages never resembled each other or that no traces of such primitive resemblance can now be found between related organisms. In all respects the same objections as those presented above may be urged against the homology of many embryonic structures and processes.

[1] *Op. cit*, p. 24.

[2] Crampton, H. E., "Experimental Studies on Gasteropod Development," *Arch. für Entwicklungsmechanik*, Bd. 3, 1896.

Numberless instances are known in which homologous adult parts arise in different ways in closely related animals—*e.g.*, the central nervous system of teleosts and of selachians, the notochord and mesoblastic somites of amphioxus and of other vertebrates, the body musculature of Lopadorynchus and of other annelids, etc.—and yet who holds on this account that there are no homologies whatsoever between any embryonic parts? The objections to such homologies are objections only to the view that they are complete and universal; among certain phyla and recognizing certain modifications, even the germ layers are homologous, and within perhaps even narrower limits there is homology of blastomeres. How else is it possible to explain the remarkable resemblances which have been pointed out between the annelids and mollusks, resemblances which are inherited with such tenacity as to be found throughout all the species, genera, and orders of an entire phylum? The fact that blastomeres are not universally homologous should not cause us to shut our eyes to certain striking homologies which do exist. Certainly within the limits here indicated the existence of cell homologies seems extremely probable, and their importance will not be overlooked save by those who are concerned only with "universal laws."

If such resemblances between blastomeres are homologies, what follows? (1) Cleavage has a certain phylogenetic significance, and, although possibly more liable to modifications than larval or adult stages and hence less trustworthy as a test of homology and of genetic relationship, it may in certain cases at least preserve ancestral conditions even after they have disappeared in end stages (annelids and mollusks). Incidentally, the homologies of cleavage added to those of embryonic and larval structures indicate the close relationship of annelids and mollusks, whereas the entire embryological history only serves to widen the gap between the cephalopods and other mollusks.

(2) The early cleavages are morphologically more important than later ones. This follows from the notion of determinate cleavage, some of the earlier blastomeres being destined to form entire regions or organs of the animal, but principally

from the fact that the earlier cleavages are more constant than the later ones. In all gasteropods, lamellibranchs, and annelids, so far as known, the early cleavages are almost identically the same; but in later stages there are certain differences in the cleavage of various species and genera, many additional cells, for example, being found in large eggs which are not found in small ones. Thus, whatever the size of the egg, three and only three quartettes of ectomeres are formed, which in all cases occupy relatively the same positions and give rise to the same organs. This is a fact of the widest application and of the highest significance; it occurs in equal and unequal cleavage and in eggs varying in size from a few microns to more than a millimeter in diameter. However, in the subdivisions of these quartettes marked differences sooner or later appear. In Crepidula plana, fornicata, convexa, and adunca the relative volumes of the eggs are as 1, $2\frac{2}{5}$, $8\frac{3}{4}$, $27\frac{2}{5}$, and yet up to the 52-cell stage there is not a single difference in the cleavage of these four species; but at this stage a single additional ectoderm cell appears in the large egg of C. adunca, due to the additional subdivision of one of the ectomeres; at the 82-cell stage there are three additional ectomeres; at a similar stage all the other species have the same number of cells, that is, three less than adunca, but in later stages the ectoderm cells divide more rapidly in all the large eggs than in the small ones, for at the time of the closure of the blastopore the number of ectoderm cells in the four species, plana, fornicata, convexa, and adunca, are in the following ratio: 1, 1.6, 2.6, 5. Finally, in the adult condition these proportions are reversed, the largest egg giving rise to the smallest individual with the smallest number of cells.

This difference in the number of cells offers no difficulty to the doctrine of cell homology unless we assume that all divisions are differential, a thing which we know is not true. After blocking out the protoblasts of various regions and organs an indefinite number of non-differential divisions may occur either before or after the complete differentiation of the parts, and this probably explains the larger number of cells in the embryo of C. adunca and the smaller number in the adult. In fact,

after the complete differentiation of all the tissues and organs, the number of cells may vary greatly in different individuals of the same species or in the same individual at different times. In adult Crepidulas the number of cells varies directly as the body size varies, the cell size remaining practically constant. These later divisions, in the main, are non-differential, and likewise it is probable that in the later stages of cleavage many non-differential and inconstant divisions occur. Not only is there greater variation in the number and size of cells in later as compared with earlier stages of cleavage, but there is also greater variation in the direction and time of division; all of which goes to prove that the earlier cleavages are more constant, more frequently differential, and therefore morphologically more important. This view, though reached by a different line of reasoning, is in entire agreement with Watasé's [1] conclusions, and is opposed to those of Wilson.[2]

At first thought it may seem strange and improbable that the earlier cleavages should be more important than the later ones. It is generally, and I think truly, believed that processes of differentiation increase in extent as we approach the end stage. However, the greater differentiations of later stages are dependent upon the lesser differentiations of earlier ones, which are therefore causally the more important. Moreover, the later differentiations in general are not phenomena of individual cells, but of cell aggregates, whereas the differentiations of cleavage are primarily differentiations of individual cells. The mosaic character of cleavage is, therefore, most pronounced in early stages, whereas the cellular phenomena of differentiation become less prominent as development advances.

[1] *Op. cit.*, p. 38.
[2] *Op. cit.*, p. 36.

THIRD LECTURE.

THE CENTROSOMES OF THE FERTILIZED EGG OF ALLOLOBOPHORA FOETIDA.

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BEFORE we discuss the centrosome we must glance at the attraction sphere, the structure of which the centrosome is a part (Fig. 4).

A typical attraction sphere has at least three essential parts: first, the relatively central, opaque body or bodies, — the centrosome or centrioles; second, the less opaque substance which forms a relatively large part of the entire attraction sphere, — the archoplasm; and, third, the rays of the attraction sphere, which in some cases extend quite to the periphery of the cell. In addition to these three structures, we often see a lighter area between the centrosome and the archoplasm, — the "Hof" of German authors and "zone médullaire" of Van Beneden. This appearance has been pronounced by some investigators to be an artifact — to be due merely to the fixatives — and is assumed, therefore, not to be a normal structure. But the centrosome itself has been called an artifact; and, again, the specific nature of the archoplasm has been denied, while some investigators see spheres or centrosomes without rays. Thus, if we accept all these denials, we shall have no attraction sphere at all. This certainly would simplify the subject; but at the present stage of the centrosome question I believe that we are not justified in assuming that any one of these structures is an artifact.

Each one of these parts of the attraction sphere has given rise to more or less discussion; but the chief interest lies in that tiny structure, the centrosome.

More than twenty questions have been asked concerning it, and if any one of you could give a final answer to any one of them, you would aid greatly in solving the problem.

What is the centrosome?

What is it morphologically? Is it one solid body that even with the highest powers cannot be resolved into more than one? Or is it an aggregation of small bodies? What is its origin? Is it of nuclear origin? — is its substance chromatin or is it nucleolar substance? Is it of cytoplasmic origin, — merely a condensation of cytoplasmic network? Is it furnished by the spermatozoön? *Is it a permanent organ of the cell*, such as the nucleus? Is it always in the cell during the resting stage as well as during division, or is it formed anew at the period of division?

What is its function? Is its presence necessary to cell division, or is its appearance merely the result of cell division?

These are merely specimens of the questions that can be asked, and every one of these opposing questions has been answered *in the affirmative*, and every one has been answered *in the negative*, by one or more investigators. They show us how far biologists are from an agreement on this subject.

If we extend our questions to the attraction sphere, we must ask: *Is there such a thing as archoplasm in the attraction sphere?* Some investigators tell us that archoplasm is not a specific substance in the cell, that it is merely a condensation of the cytoplasmic network, merely a delusion, and that the very term should be dropped from the cytological vocabulary. In the egg of Allolobophora foetida this "delusion" can be sharply differentiated from the cytoplasm by differential staining. Assuming that the archoplasm *is* a specific substance, it is asked: Are the rays of the attraction sphere archoplasm, or are they cytoplasm? And each of these questions has been answered in both the affirmative and negative.

In studying the centrosomes of the fertilized egg, we are brought face to face with the problem of the relative values of the so-called egg and sperm centrosomes (Fig. 3). Some investigators have asserted that in certain animal forms there is no egg centrosome, and it has been suggested that in the cases where it is unquestionably present it is merely a phylogenetic reminiscence, an out-of-date structure. (Allolobophora foetida must be an extremely old-fashioned worm, for both its maturation spindles possess this relic of the past.) (Figs. 2, 3, 4.) Other investigators find the centrosome present during the constricting off of the polar bodies; but after the second polar body is formed the attraction sphere totally disappears and does not reappear in any form; the sperm attraction sphere, on the contrary, grows, becomes more and more pronounced, divides, and forms two daughter attraction spheres, which con-

FIG. 1. — Spermatozoön, showing spine, head, middle-piece, and tail.

tinue to move away from one another until each occupies a pole of the first cleavage spindle. This, you see, involves the important assertion that the sperm centrosome is the ancestor of all the centrosomes of the individual; for after each division the mother centrosome is said by many investigators to divide and to form the daughter centrosomes for the next division.

These observations regarding the important rôle played by the sperm attraction sphere involve most to those who hold certain definite views regarding the male centrosome. They hold that the male centrosome is furnished by the spermatozoön itself; that it is the middle-piece of the spermatozoön before the spermatozoön enters the egg (Fig. 1); that after entering the egg, the middle-piece contributes the substance which becomes the centrosome of the so-called sperm attraction sphere (Fig. 3). Thus, you see, according to some observers, the middle-piece of the spermatozoön furnishes the substance which forms all the centrosomes of the individual. They do not allow that the egg even makes a contribution.

There is a third view regarding the relative values of the egg and sperm centrosomes. You are familiar with it under the name of "Fol's quadrille of the centres." This view has been attacked repeatedly during the past year; in fact, the attack on the "quadrille of the centres" might be appropriately called

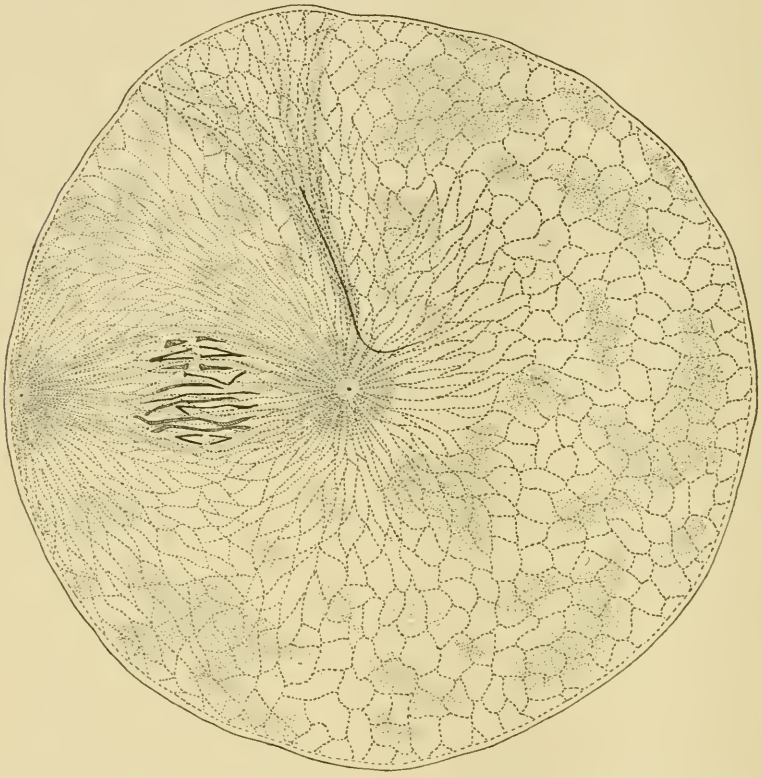


FIG. 2. — Optical section of entire egg, showing head of spermatozoön, fertilization cone, first maturation spindle with attraction spheres and archoplasm in the spheres, cone, spindle, and throughout the cytoplasm (microsomes not represented).

the latest cytological fad. It seems to be the fashion, "the mode" (they do us biologists great injustice when they accuse us of scorning such things).

It seems to me that discussion as to the rôle played by the egg and sperm attraction sphere is of no especial value until we know something more definite concerning the origin of their two centrosomes. Has the male centrosome a different origin

from the egg centrosome? Is the male centrosome the *middle-piece*, or any part of the middle-piece, of the *spermatozoön?* The phenomena of fertilization in the egg of Allolobophora foetida warrant a negative answer to this question. I am aware

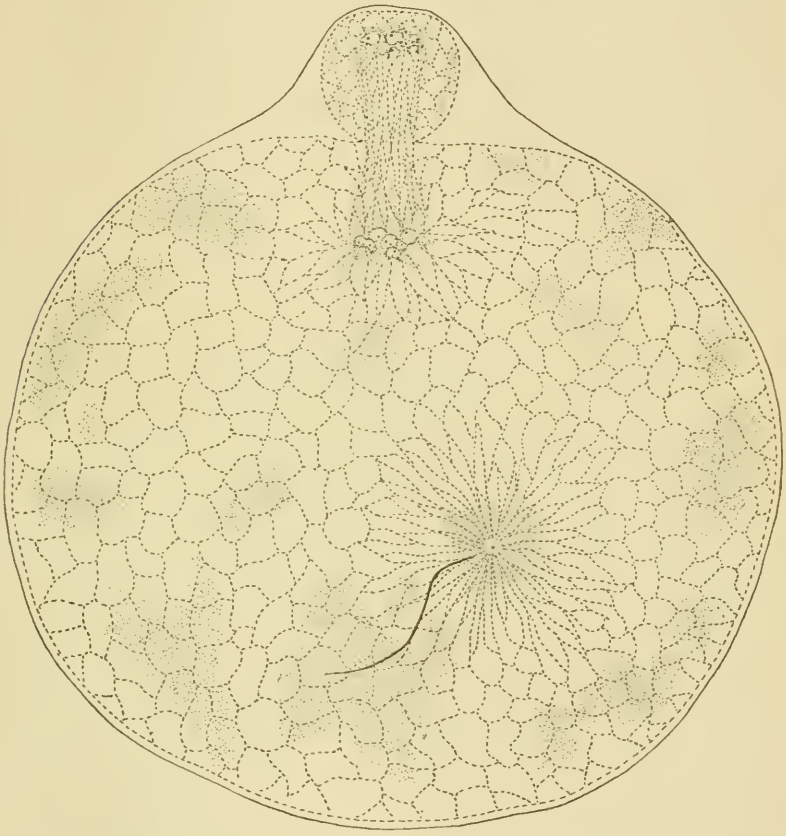


FIG. 3. — Optical section of entire egg, showing telophase of first maturation spindle, head of spermatozoön, with male attraction sphere and archoplasm in the sphere, spindle, and throughout the cytoplasm (microsomes not represented).

that a denial of such a generally accepted view demands the strongest evidence for its support, and I confess that the only evidence I can at present produce is that of differential staining. One of the facts justifying the assertion of the identity of the male centrosome with the middle-piece of the spermatozoön is that both structures have been shown to select the same

stain. But in the egg of Allolobophora foetida I have been able, by two different methods, to differentiate the two structures. Staining substances differently is a relatively safe method; but staining substances alike in order to prove their identity is a very dangerous one. We all know numerous examples where this method proves to be a weapon which shoots backwards and tempts us to assert relationships where they do not exist. But we must not forget that even differential staining is not entirely trustworthy; for chromatin has been shown to select different stains at two different stages of its development, and yet we do not question its being chromatin at either stage. I hope to be able to support the evidence of differential staining by tracing the fate of the middle-piece after it enters the egg.

A careful, and I trust conscientious, study of the sperm attraction sphere of the egg of Allolobophora foetida has led me to the following conclusions: I believe that all its parts (centrosome, archoplasm, and rays) are morphologically the same substances as the corresponding parts of the egg attraction sphere, and that each one of these parts is merely an aggregation of a substance existing throughout the cytoplasm (Figs. 2, 3, 4). I believe that the sperm attraction sphere is a cytoplasmic phenomenon just as much as the fertilization cone is a cytoplasmic phenomenon (Figs. 2, 3). Why cannot the sperm attraction sphere be an expression of a definite effect produced upon the cytoplasm by the entrance of the sperm, just as the fertilization cone is a cytoplasmic phenomenon which does not appear until the sperm enters the egg?

Let me compare the two phenomena, the fertilization cone and the sperm attraction sphere. In this egg both structures appear to depend not alone upon the entrance of the spermatozoön, but also upon a definite stage of development reached by the egg; the cone is never found after the first polar body is constricted off,[1] and the sperm attraction sphere is never found

[1] After examination of nearly one thousand eggs, I have found only a few in which the head of the spermatozoön is penetrating the egg after the first polar body is formed, and in none of these cases have I found a cone; but it is possible that the cytoplasm of these eggs may not be entirely normal, though it appears to

before the first polar body is about to be constricted off, no matter how far the spermatozoön may have penetrated into the egg (Fig. 2). And this feature is not confined to this egg; for in studying the literature I have not been able to find any satisfactory evidence of the appearance of a sperm attraction sphere earlier than the anaphase of the first maturation spindle. On the contrary, it is distinctly stated that in those cases where the egg is fertilized very early (before the first maturation spindle is formed), the sperm remains unchanged (sometimes for

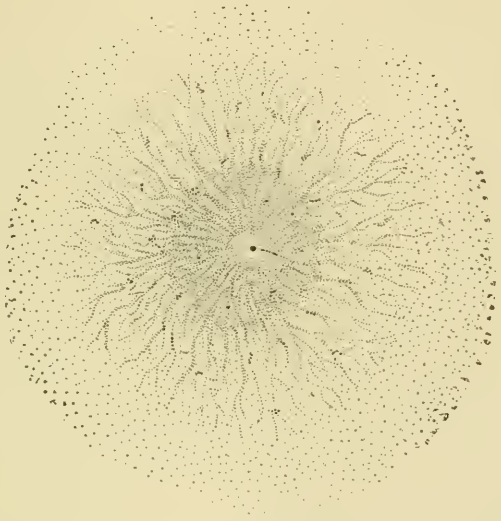


FIG. 4. — Male attraction sphere, showing cytoplasmic network, archoplasm, centrioles, and some of the microsomes.

hours) until the first polar body is constricted off; that there is no interchange of action between the sperm and egg until the first polar body is formed.

To continue the comparison between the fertilization cone and the sperm attraction sphere: In examining the figures you will find that both structures contain a substance not confined to them but distributed throughout the cytoplasm (Figs. 2, 3, 4). (In these figures this substance is represented by the gray

be so. This possibility is suggested by the fact that the structure found by Fick in the egg of Axolotl, and which is similar to the fertilization cone of Allolobophora foetida, appears normally after the first polar body is formed.

stippling, and in the preparations it is stained blue.) Again, you will find that the rays of the attraction sphere and the network of the cone appear to be formed of a substance not confined to these structures but forming the cytoplasm of the entire egg. (In the preparations from which these figures were drawn this substance stains red.) Again, the substance which forms the centrosome or centrioles in Fig. 4 appears to be only a part, an aggregation of a substance distributed throughout the cytoplasm. By two different methods I have been able to differentiate these microsomes from the rest of the cytoplasm and archoplasm of the egg.

Thus we have in this egg at least three cytoplasmic elements, — cytoplasmic threads, archoplasm, and microsomes. This recalls Schloter's work on certain gland cells of Salamander, where he differentiates a like number of cytoplasmic elements.

I have now shown what appears to me to suggest a like origin — an entirely cytoplasmic origin — for the two structures (the fertilization cone and the sperm attraction sphere), and in doing this I have shown the points of resemblance between the two structures. Now let me show wherein it appears to me they differ.

In one case the anterior end of the head of the spermatozoön seems to produce the effect upon the cytoplasm expressed by the fertilization cone; and in the other case the middle-piece seems to produce the effect upon the cytoplasm expressed by the attraction sphere. We have a cone the moment any part of the head penetrates the egg; if the head penetrates only a short distance, we have only a small cone; when it penetrates farther, we have a more pronounced cone. Thus only the anterior end of the head of the sperm is necessary to produce the fertilization cone; the cone can be formed *before* the middle-piece enters the egg. On the contrary, the sperm attraction sphere cannot appear until a relatively large part of the spermatozoön has penetrated the egg, until the middle-piece as well as the head has entered into the cytoplasm.

One cannot avoid seeking some explanation of the fact that each end of the head of the spermatozoön produces a cytoplasmic phenomenon within the egg. If we recall those

accounts of the development of the spermatozoa where part of the archoplasmic mass in the daughter cells of the spermatocytes, second order, forms the spine of the spermatozoön, as well as its middle-piece, may we not regard the head (including the spine and the middle-piece) as an attenuated spindle? And may we not expect each end of the spindle to produce an effect upon the cytoplasm similar to the phenomena at each end of the spindle in the cytoplasm of the spermatocytes? Would not such a phenomenon produced by a *moving* body cause a structure like the fertilization cone? It seems to produce the effect for only a definite time, possibly during the fusing of the substance of one pole (the spine) with the egg cytoplasm; for, finally, the head moves out of the area of the cone, leaving it behind.

This suggestion of a possible explanation is obviously without value unless we find a fertilization cone and a sperm attraction sphere in *all* eggs where the spermatozoön has a spine and a middle-piece; for example, in the spermatozoa of Axolotl and Allolobophora foetida we have the spine and middle-piece, and in the egg of both these forms we have the fertilization cone and the sperm attraction sphere. In Myzostoma we have neither spine nor middle-piece, and we have neither fertilization cone nor sperm attraction sphere.

The fact that the attraction sphere does not appear until the middle-piece enters the egg has served to justify the assertion that the centrosome of the sperm attraction sphere is of the substance of which the middle-piece is formed. (The fertilization cone does not appear until the head of the spermatozoön enters the egg, but we are not tempted to say that the head breaks up and forms the cone, for the simple reason that the head remains intact.)

The centrosomes of Allolobophora foetida (as they appear to me) furnish a strong support for the view of Dr. Watasé and others as to the strictly cytoplasmic origin of the centrosome. I am not aware that Dr. Watasé has definitely stated that the sperm attraction sphere is of cytoplasmic origin, but his paper on the "Homology of the Centrosome" certainly implies it. In the egg of Allolobophora foetida, however (Fig. 4), these little

bodies (one or more of which apparently take part in forming the centrosome) do not appear to be merely thickenings of the cytoplasmic threads (this, you remember, is an essential element of Watasé's theory); on the contrary, many of them appear to be scattered throughout the cytoplasm in a relatively independent

Fig. 5. — Optical section through entire egg, showing telophase of second maturation spindle and head of spermatozoön forming male pronucleus. Male attraction sphere has disappeared. Egg attraction sphere has nearly disappeared (microsomes not represented).

way. They vary, too, greatly in size, some of them being relatively very large and unmistakably independent of the cytoplasmic network, but, as no exact distinction can be made as to size and they all stain alike, I do not feel justified in assuming that the smallest ones and the largest ones are of different origin, though many of the smallest ones appear to be imbedded

in the cytoplasmic network and to represent transverse sections of the cytoplasmic threads.

This egg might be subpoenaed as a witness for the theory that the centrosome is a mechanical centre which appears only during the so-called active stages of development. The egg attraction sphere is present during the two maturation divisions; but after the second polar body is formed and the female pronucleus begins to develop (Fig. 5), it totally disappears. The sperm attraction sphere is present until the head of the spermatozoön begins to develop into the male pronucleus and then it also totally disappears (Fig. 5). Both spheres are absent during a relatively long period (that is, while the young pronuclei are developing), and when the pronuclei have attained their maximum size, two attraction spheres appear again in the cytoplasm, and the cleavage spindle is formed.

If we believe that both attraction spheres are cytoplasmic phenomena, that the constituent parts of each are made up of the same cytoplasmic elements (that is, that they are alike morphologically), and that they differ only in that different conditions are necessary to the appearance of each, two questions suggest themselves: First, if the two spheres are alike, why does a later stage of development of the egg seem to be necessary to the appearance of the male attraction sphere, why does the latter not appear as early as do the first maturation spheres? It seems, however, that it does not (and this is true not alone of this egg). Does this indicate a difference in the attraction spheres themselves, or does it indicate a definite change in the cytoplasm?

In this connection it is interesting to note that the structure of the cytoplasm before the polar bodies are formed differs somewhat from its structure after the polar bodies are formed. At the earlier stage the meshes of the network are very much closer and at the later stage they are more open (alveolar) in structure, this condition bearing a definite relation to the periods of rest between the divisions and reaching its acme at the pronuclear stage just before the cleavage attraction spheres appear.

Another puzzling question suggests itself at least to a practical observer — a question of economy. If the two spheres

are alike, why is the second necessary? why cannot one do the work of both? The apparent extravagance seems quite justified, especially if we grant that the attraction sphere is indeed an attraction sphere, an expression of force, and that it is as necessary to the sperm as to the egg. If the sperm must depend upon the egg's attraction sphere, it is apparently hampered by at least two conditions: it must penetrate far enough into the egg to be within "working distance" of the egg attraction sphere, and it must penetrate at the right time, that is, while the egg attraction sphere is present. (In this egg, you remember, and in many other forms, the egg attraction sphere disappears at a definite time, that is, after the second polar body has been formed.) If, however, the sperm has its own attraction sphere, it is not hampered by the above-mentioned conditions as to space and time, and a study of the literature shows that it does enter at very different stages of the development of the egg, in some forms even while the germinal vesicle is intact, and in many more forms as late as after the second polar body is formed; if it enters too early, it simply waits at any point in the egg for its attraction sphere (until the anaphase of the first spindle) and if it enters late its attraction sphere forms at once at the periphery. If these observations are of any value, they suggest that the sperm is relatively independent as to the exact time of its entrance and the distance it must penetrate, and that thus the egg has a much better chance of being fertilized; it would be poor economy for it to save an attraction sphere and lose a sperm.

There seems to be at least one case in which the egg attraction sphere does do double work. Dr. Wheeler's work on Myzostoma has shown us that at no time during fertilization does an attraction sphere appear in connection with the sperm, and it is interesting to note that this egg is fertilized very early while the germinal vesicle is still intact. (The spermatozoön takes no risks of arriving too late to utilize the egg attraction sphere.) Another observation of Dr. Wheeler's on this form is extremely interesting: The spermatozoön has no middle-piece — a very significant circumstance (as Dr. Wheeler says) in connection with the fact that there is no sperm attrac-

tion sphere. You remember that in the egg of Allolobophora foetida (and this is true of a great many forms) there is no sperm attraction sphere until the middle-piece enters the egg. Thus the spermatozoön's having no middle-piece is in entire accord with the fact that after it has entered the egg we find no sperm attraction sphere.

It seems to me that we must study the centrosome under the microscope to arrive at even approximately definite ideas regarding these puzzling questions. We need our own observation to guide us through the labyrinth of conflicting views. If one studies the attraction sphere through the literature alone, the different theories and the shades of disagreement between the numerous authors make any definite conception of the subject very difficult. I should suggest a sort of centrosome creed, and then you can change it every time you read a new paper on the subject. If you do not read too fast, you will perhaps not have to change it oftener than forty times a year.

My creed just now — just now, remember, this minute — is something like this:

I believe in the centrosome.

I believe in *two* centrosomes, the *egg* centrosome and the *sperm* centrosome.

I believe that the centrosomes of *both* sperm and egg are cytoplasmic elements — and so on.

I could make a very long creed; but the final article must be:

I believe I really *know* very little about the subject, and when I have read more I shall probably know less.

FOURTH LECTURE.

THE METHODS OF PALAEONTOLOGICAL INQUIRY.

W. B. SCOTT.

It is one of the misfortunes connected with the vastly expanded knowledge of nature which characterizes the present era, that the capacity of the human mind does not expand in equal proportion. No one can ever hope to grasp the full meaning of the enormous and ever-growing accumulations of facts, and the investigator is compelled, whether he likes it or not, to become a specialist and to devote himself to the cultivation of a narrow field. The manifold disadvantages which necessarily accompany such a division of labor are obvious and need no commentary here. Suffice it to mention that one such drawback, which has profound and far-reaching effects, is the loss of sympathy and "touch" between workers in closely allied subjects. The investigator can, therefore, render useful service to his fellows in other fields of inquiry by occasionally bringing before them the results which he has attained, and in pointing out the questions of common interest to which all may contribute.

It is not enough, however, merely to exhibit results, even though stripped of all technical verbiage and made thoroughly clear and intelligible; the methods by which these results have been reached must also be made perfectly plain and submitted for examination. We all have a healthy skepticism regarding methods of which we are quite ignorant, unless they happen to be mathematical, when they are apt to be accepted unquestioningly and blindly, as though they were the oracles of the gods.

In view of this fact, I have thought that it might be of interest to an assembly of biologists to give an account of

some of the methods of investigation in vertebrate palaeontology, a large subject, only the more salient points of which can be touched upon in an hour's talk. Judging from the questions that are asked me and from the letters that I receive, it would seem that these methods are a mystery and a sealed book to workers in other departments of morphology, and yet there is nothing mysterious or recondite about them. They consist simply in the application of patience, common sense, and manual skill to the problems which confront us. The collector and the museum preparator do the greater and heavier part of the

FIG. 1.— General view of White River Bad Lands. (Photograph by Williston.)

work; to the investigator falls the pleasanter task of studying the material which has been gathered and made ready for him.

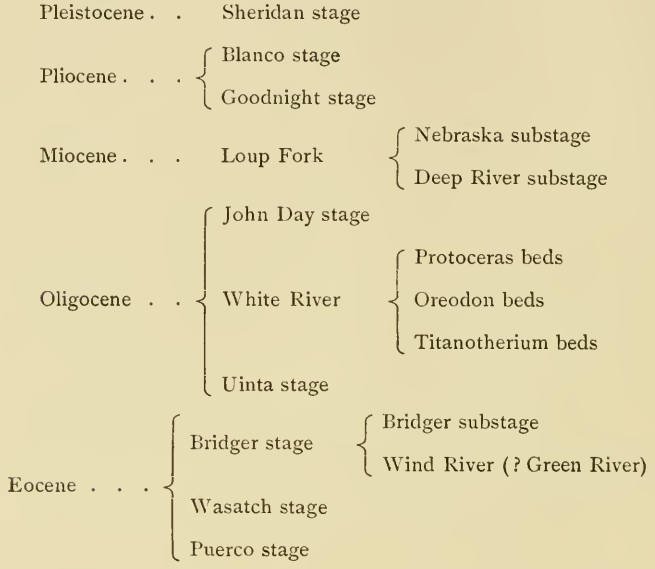
The indispensable prerequisite for the scientific study of extinct forms is to determine the order of succession in which those forms made their appearance upon the earth. If we study the animals without reference to this order of succession, we may learn much, it is true, but many of the interesting problems will remain insoluble, and our ideas of phylogenetic relationship will surely become confused and hazy. It is not always easy to distinguish a degenerate from a primitive form, unless we know its history, and history without chronology is a chaos. Consequently, the first step to be taken in our inquiry

involves a geological problem, and consists in determining the order of formation in time of the rocks which contain the fossils. It is only of late years that the extreme importance of exact accuracy in this determination has become apparent. Formerly it was regarded as sufficient if we could determine a fossil as Cretaceous or Eocene, but now we need to know its precise position and range in the geological column. This is because we now endeavor to trace out the phylogenies step by step through every gradation, and it is only this humble, plodding, step-by-step method upon which any dependence can be placed. Brilliant generalizations and bold hypotheses may be of great service, but if they are to endure they must be verified in every particular by the more laborious but surer method. Darwin's motto, "It 's dogged as does it," applies here in its fullest force.

Not to scatter our energies in attempting hurriedly to survey too wide a field, it will be well for us to confine our attention entirely to the Tertiary period of geological history, and in what I have to say I shall deal only with the mammals, the principles being the same as for other vertebrates. It is the good fortune of the American palaeontologist that in the western states and territories occurs an almost unbroken succession of fresh-water formations, from the end of the Cretaceous throughout the Tertiary period, and in these hardened sands and clays has been preserved a marvellous wealth of the remains of the successive faunas and floras which inhabited the land. Not all of these formations have yet been investigated, and hardly any of them have been mapped, but enough is already known to provide an accurate outline of historical events in the development of the continent.

The sure method of determining the chronological succession of strata is that of observing their order of superposition, a method which is not always practicable, but which is infallible wherever it can be applied, and which is simplicity itself. The principle is merely that in a series of undisturbed strata the order of superposition is the order of relative age, the oldest being at the bottom and the newest at the top. Fortunately, this sure and simple method is applicable to most of the western Tertiaries, and hence their chronological order may be

established beyond cavil. The following table gives this order of succession of the principal fresh-water Tertiaries, omitting a few that are not yet sufficiently well known for exact reference.



The classification employed in this table is a little different from any that has yet been published, a difference which principally affects the Oligocene. Usually the John Day is called Lower Miocene; the White River, Oligocene, and the Uinta, Upper Eocene. The arrangement adopted in the table corresponds to the newer classifications of the Oligocene made use of in France, and has the further advantage of exhibiting the close faunal connections between the Uinta, White River, and John Day stages, an unbroken succession such as no other three formations display. When these three successive faunas shall have been recovered, reconstructed, and thoroughly studied, we shall have an ideal set of phylogenetic series, which will throw a brilliant light upon the processes of evolution. The beginning which has already been made in this work encourages us in really enthusiastic expectations. Abstractly, it matters little whether we call these beds Eocene or Miocene,

but concretely it is of the highest importance that they shall be so named as to exhibit their relationship to the contemporary formations of other continents. The problems concerning the origin and migrations of genera, and the geographical distribution of mammals in general, can be solved only when the chronological relations of geological horizons in different continents have been established. It is therefore necessary to use classifications which shall not obscure these relations, and the conservative terminology of some American writers has so far misled European observers as to vitiate much otherwise excellent work. For this reason I have preferred to follow the French classification, even though it should introduce rather startling innovations in our current systems.

Time would utterly fail us to consider the whole of even the Tertiary formations, and of these we must make a selection. For our purpose none of the horizons is more suitable than the White River. It is, in the first place, the classic ground which yielded to Leidy and Owen the materials for their epoch-making studies; it has been repeatedly explored for more than half a century past, and is, therefore, the most thoroughly known of all the formations, and it is much the richest in satisfactory and well-preserved fossils. Finally, it happens to be the horizon with which I am, personally, the most familiar, and therefore speak of from a somewhat extended experience.

The White River deposits offer many problems to the geologist which have not yet been solved, but into which it is not necessary for us to enter. It will be convenient to consider the body of water in which the beds were laid down as a lake of fluctuating size, which at one time or other had a very great extension. It covered northeastern Colorado, following the foothills of the Rocky Mountains westward into central Wyoming, sweeping thence along the southern edge of the Black Hills of South Dakota, and eastward for a great, but as yet unknown, distance into the plains, and covering very large areas in Nebraska and South Dakota. Other areas of the same beds in North Dakota may represent the same body of water, the intervening strata having been swept away by denudation, but this is still uncertain.

Into this great body of water the streams incessantly brought quantities of gravel, sand, clay, and mud, which were sorted out by the still waters of the lake and deposited in layers, which, however, are often irregular, changing from point to point in a very puzzling way. The strata are, for the most part, only imperfectly indurated and quite soft, so that they may be readily cut with a knife, though occasionally they are rather hard, especially the sandstones. The semi-arid climate, which has prevented the growth of any dense covering of protective vegetation, has carved the thick masses of strata into the most curious and fantastic forms, known as "Bad

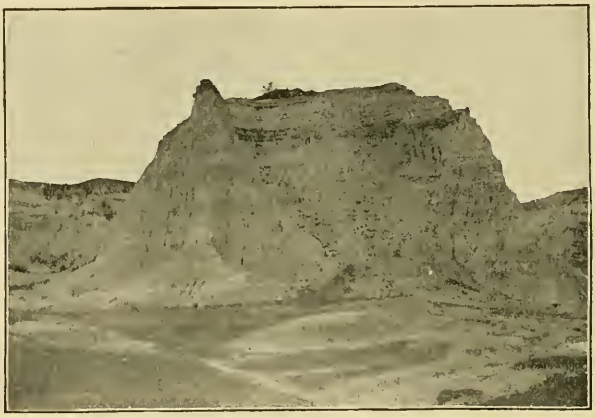


FIG. 2. — Butte in White River Bad Lands.

Lands." This term is an abbreviated translation of the phrase "mauvaises terres à traverser," given by the early French explorers to express the extraordinarily rough and broken nature of the country. It must not be supposed that all bad lands are composed of White River rocks; on the contrary, we find them in all of the later geological formations, from the Cretaceous onward, the conditions for their formation being altogether physical in character. Still, the White River Bad Lands are among the most striking and peculiar of them all. The outlook from any high point over these Bad Lands is a scene long to be remembered; vast masses of the strata have been swept away by the denuding agencies, and the harder parts

which have been left standing assume the most bizarre outlines, often strikingly imitating architectural forms, towers, palaces, pinnacles, and spires of some ruined city of the giants. The weird, fantastic shapes more resemble the "baseless fabric of a vision" than the topographical forms of everyday reality.

The principal agent in this enormous work of destruction is the rain, which dissolves out the calcareous cement ($CaCO_3$) that binds together the insoluble particles of sand or clay into a firm rock. True, the total amount of atmospheric precipitation is small, but the rainfall is heavy when it does come, and often the dry water courses are in an incredibly short time converted into rushing torrents. Experience soon teaches the explorer not to put his camp on low ground, but always to select a point to which the flood waters never rise. When the rain can reach freshly exposed surfaces of rock, the disintegration is often excessively rapid. I have observed a firm rock to be thoroughly disintegrated to the depth of $\frac{1}{16}$ of an inch by a single light shower, lasting only a few moments. In the Bridger Bad Lands the Princeton expedition of 1885, in excavating the skeleton of a large *Uintatherium*, dug out a great hole, the rock from which was piled into a cairn. When we revisited the same spot a year later, the cairn was found to be weathered down into a low hummock of soil, and the hole was so filled up as to be hardly recognizable. From these observations one might infer that the progress of rock decay must be exceedingly rapid, but as a matter of fact, it is very slow. The rainfall is limited, and of even more importance is the fact that the soil produced by the disintegration of the rocks, which covers all the buttes save the vertical faces, becomes, when wet, almost impervious to water. A heavy downpour of several hours' duration will wet this soil to the depth of only two or three inches. It is this waterproof soil which throws off the rain, causing it to gather in the gulleys and water courses, and to form those sudden and violent floods which to be appreciated must be seen.

The exact forms assumed by the bad land "buttes" (or eminences), as in the case of other topographical forms, depend upon the interaction of several factors, such as the manner in

which the harder and softer beds alternate, their angles of inclination, and the intensity and character of the denuding, disintegrating agents. Most of the Tertiary formations have strata which are practically horizontal, and this lack of inclination has a decisive influence upon the resulting topographical forms. True, the western end of the White River beds is some 2000 feet higher than the eastern end, but a rise of 2000 feet in more than 500 miles, which is an average grade of four feet to the mile, or 1 in 1320, is so slight that it may be neglected. Much more effective is the manner in which the harder beds are arranged, and, as this varies indefinitely, the number of resulting forms is well-nigh incalculable, though a certain uniformity is apparent in the greater number of them.

The curious aspects of bad land scenery are much enhanced by the coloring. In the White River region the dreary, barren, and desert character of the country is emphasized by the pale, ashy gray of most of its rocks and soils, a color which the lantern slides reproduce quite accurately. Only the marvellous changes wrought by the magic touch of the tender evening lights redeem the scenery from utter dreariness. In other regions, as along Vermilion Creek in Wyoming, the most brilliant hues of reds and purples give an unearthly beauty to the weird picture.

In these days of evolutionary study almost as much importance is attached to a knowledge of the environment which surrounds an organism, as to a knowledge of the organism itself, and rightly so. Whether or not we follow Weismann in declaring that acquired characters cannot be transmitted, we cannot fail to see the dependence of organisms upon their environment, the only question being whether the effects are directly or indirectly produced. Of course, we do not hope or expect to learn the environment of extinct forms with the same fullness and accuracy as in the case of existing animals, but still we may learn much that is of importance. We may determine something of the nature of the land surfaces at the time when the organisms in question existed. The new study of topography, which is rapidly rising to the dignity of a distinct science, gives a great deal of welcome information here. Even

more important for our purposes is the determination of the climatic features, especially of the temperature and moisture. The most trustworthy instruments for this determination are the fossil plants, the evidence of which, though it must not be uncritically accepted, is yet very valuable. Thus the Eocene and early Oligocene vegetation of the interior of our continent points to the prevalence of warm climates far to the north, huge palms and other subtropical plants abounding in Idaho and Wyoming. By White River times a change had come, not extreme at all and probably slight, but yet very significant, especially in view of what was to come later. The palms have nearly or quite disappeared from the northern interior, a hardier vegetation taking their place; and the withdrawal of the great crocodiles, which had so abounded in the Eocene lakes, confirms the inference as to climatic change.

We may often learn something of the environment from the facts of geological structure, as an example will show. On the summit of the divide between the White and Cheyenne Rivers in South Dakota is a patch of conglomerates and hard, coarse sandstones, which have weathered into overhanging ledges, fantastic amphitheaters, and cirques. These sandstones represent a system of stream-channels, cut through the lake-bed. Alternations in the water stages are indicated by the clay beds, which dovetail in along the edges of the sandstones and were obviously formed at the same time as the latter. Both sandstones and clays are crowded with fossils, and both, as we have seen, were contemporaneous, and yet it is quite remarkable how different the animals are; species which are common in the clays are rare or absent in the sandstones, and *vice versa*. The explanation of this curious difference is probably to be found in the inference that the sandstones contain principally the remains of the upland fauna, which were swept down by the flooded streams and entombed in the lake, while the fossils of the clays represent chiefly aquatic forms and species which haunted the low-lying, swampy shores. That a certain amount of mingling of the species should occur was inevitable, in view of the contemporaneity of the containing strata, and certain species also doubtless ranged over the whole area, hill and plain and

swamp. The case is an interesting example of how instructive the study of the strata themselves may become from the strictly biological point of view.

So far we have been dealing with an aspect of our subject which is geological rather than biological, but which yet represents the indispensable preliminaries of any truly scientific study of palaeontology. Coming now to the aspects which deal more directly with the latter, we must obviously begin with the subject of collecting. There is all the difference in the world between good and bad collecting, and the work of

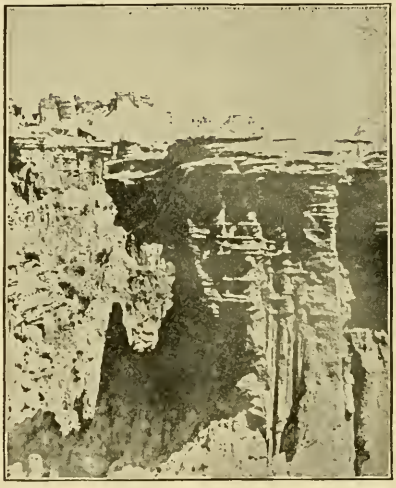


FIG. 3. — Sandstones formed in old stream-channels; White River Bad Lands.

the careless or incompetent collector is so mischievous, so exasperating, so destructive of valuable material, that one is often tempted to wish that the work might be prohibited to all save thoroughly trained and careful men. Of course, the first step in collecting is to find something. I find the impression very widely spread that the collector goes out into the bad lands and begins to dig at random, until he happens upon a bone. If he were to undertake his work in such a foolish way, experience would soon teach him that he might employ his time more profitably in any other possible calling. The specimens must be found by surface indications. In order to do this, the

ground must be examined by traversing it along such lines as will best expose the surface to the eye of the seeker, and some of the best workmen make their preliminary examinations of the ground and "locate their finds" on horseback. The extraordinary climbing powers of the western broncho make him an invaluable adjunct in the work. This bone-hunting requires for its successful prosecution great keenness of vision and that trained aptitude which enables the hunter to rapidly but thoroughly examine the ground, not allowing the glance merely to wander over the surface, but concentrating the attention upon every successive square rod. The silicified bones are harder than the rock or matrix which contains them, so that the process of weathering leaves them standing in relief; but, as the weather is destructive to the fossils also, the longer a specimen has been exposed, the more injured it is. A consequence of this is that the most desirable specimens are those which are the hardest to find, because least exposed.

When a fragment of bone is seen, it may prove to be the guide to a whole skeleton, and therefore no indication can be neglected. If the fragment is lying loose upon the surface, it must be traced to its parent ledge, remembering that it has been washed downward, and a line of fragments will lead the collector to the spot whence they have all been derived. More favorable is the case where the visible fragment is still in place and is the only portion of the specimen exposed, the rest being concealed in the shelter of the rock; such concealed specimens are almost always the best. When excavated, the specimen may prove to be a few teeth, a limb bone, a skull, a complete limb or foot, or even a whole skeleton; of course, skeletons are rare and constitute the great prizes of the collector. At first sight, it may seem puzzling why a skeleton should be preserved nearly or quite intact in one case, and in another only a single bone should be found; to understand this we must consider something of the conditions under which animals are fossilized.

When a land mammal is drowned, the body, being somewhat heavier than water, sinks to the bottom at once, though a swift current may transport it for considerable distances. When it finally comes to rest upon the bottom, the rapid deposition of

sand, mud, or other sediment upon it will, if sufficient in quantity, bury it completely and prevent its being scattered, and thus fossilize it as a skeleton. If, on the other hand, the carcass is only lightly weighted by silt, it will rise to the surface, when the gases engendered by decomposition begin to inflate and distend the abdominal walls. Floating thus, being pulled about and partially eaten by carnivorous fishes and reptiles, it will drop a limb here, a jaw there, a few vertebrae in another place, until the fragments are scattered over a wide area of the lake bottom.

In any case, when a specimen is taken at all, the cardinal rule of collecting is to take the whole of it, not allowing the smallest recoverable fragment to escape. It is surprising to see what great importance tiny fragments may assume, when the work of piecing together the broken bones is undertaken; the presence or absence of such a fragment may determine success or failure in this patchwork. The most unpromising heap of fragments may often be converted by skill and patience into beautiful specimens, not, as the uninitiated sometimes suppose, by the liberal employment of the imagination and plaster of Paris (though this has been done), but by the actual fitting together of the broken pieces of bone. The careful collector knows all this, and spares neither time nor pains to find all the fragments which have been weathered out, even washing and sifting the soil, when necessary for his purpose.

When the fossil has not suffered from the weather, but remains intact, the manner in which it can best be taken up will depend upon a variety of circumstances, and especially upon the firmness of the rock and of the bones. If the rock is fairly hard, not traversed by many or irregular joints or cracks, the best method is carefully to expose enough of the specimen to determine its size, and then with pick, or hammer and chisel, cut a deep groove in the rock all around the fossil, making sure that the groove is deep enough to clear the bones, then by driving wedges beneath the block thus isolated, raise it in one mass. If the fossil is too large to be handled in one piece, it may be taken up in several blocks and packed for transportation.

Often, however, the rock will not endure such cavalier treatment; it is traversed in every direction by fine joints which divide it into innumerable minute blocks, and, as the same joints go through the fossil, the whole would fall into irretrievable ruin, were it loosened by wedges; or the matrix may be incoherent and the bones soft and crumbling. In such cases a method devised by Mr. Hatcher may be employed with full assurance of success. This method consists in exposing the fossil inch by inch with fine, sharp tools, and when a sufficient surface has been laid bare, a strip of muslin soaked in flour paste is pressed upon the exposed area, and the process is then

FIG. 4. — Getting out a Titanotherium skull.

repeated until the whole upper surface is covered by the pasted strips. Layer after layer of the strips is pasted on, the layers crossing at right angles, and they soon dry and stiffen until they become as hard as a board. The pasting is then extended to the sides, and when these have been properly treated, the block may be turned over and pasted upon the lower side, completing the process by winding strips of coarse sacking, also soaked in paste, around the whole block, until it is perfectly protected by a rigid case, and will endure transportation and rough handling indefinitely. By this most useful method very hopeless-looking specimens may be saved and converted into highly valuable

material. It need hardly be said that careful packing is an indispensable necessity, and to this end the collector should not only have ample supplies of cotton, tissue and wrapping paper, but will find it useful to keep lumber in his camp and make his boxes on the spot as he needs them. Usually the fossils must be hauled long distances to the railroad, and they will carry much better if boxed ready for shipment than in any other way.

Having now gathered our fossils and brought them into the museum, it remains to make them available for study; this is the work of the museum preparator, and is often exceedingly tedious and laborious, calling for a very high degree of both skill and patience. In case the bones are hard and firm and enclosed in a hard matrix (the two usually go together) the matrix must be removed by the use of fine chisels and needles. If the rock is not too hard, a very useful tool for the work is a sewing-needle set in a handle; such tools, it is hardly necessary to say, make the work very slow and call for unlimited patience, but haste emphatically means waste in dealing with fossils. Great care is required in this work, for the bones are apt to be more or less displaced and scattered, and they often turn up where they are least expected. An incautious blow may do irreparable mischief. Very soft bones must be treated with alcoholic solutions of glue, which readily penetrate into the pores and set into a firm mass, making the specimens almost as hard as recent bones. Fragmentary specimens are laboriously pieced together — most tedious work, but work which is often richly rewarded by making heaps of irregular fragments grow into beautifully complete specimens.

The pasted blocks require skillful handling; the strips may be removed by finding the end of one and slowly pulling it off, aiding the process, if necessary, by a damp sponge, which softens the paste. As soon as the bone is exposed and a loose fragment is seen, the fragment is at once lifted out, cleaned, and cemented back in its place, when a new surface is laid bare and treated in the same way. In this fashion it is possible to save a specimen which, if allowed to break up, would involve a hopeless task in piecing it together again.

All the processes described and all the labor, skill, and

patience expended are means to the end for which the whole has been undertaken, namely, the comparative study of the material. For this purpose it is hardly possible to gather specimens enough, for almost every individual will show something which others will not, and in looking over a great collection, one is tempted to believe that there are no duplicates and that nothing can be spared. Before attempting to make out phylogenies, it is well to determine the complete dental and osteological structure of every available species. From the popular standpoint this is being righteous overmuch and taking most superfluous pains and trouble. The palaeontologist is believed to be able to reconstruct missing types from the merest hint, a single bone or tooth, a scale or feather. In current literature no supposed scientific method is more frequently cited by way of illustration than this, *ex ungue leonem*, etc., and yet nothing could be more absurd. This superstition, for it is nothing else, seems endowed with perpetual youth and vigor, and no amount of exposure suffices to kill it; doubtless it will continue to flourish for centuries. It may even be true that the instinctive distrust of palaeontological results which many morphologists feel, is due to this prevalent notion of palaeontological methods; careful workers cannot be expected to put any trust in such easy-going ways of investigation, if they may be dignified by that name.

Fortunately, the single-bone method of reconstruction is not a practicable one. I say fortunately, because if that method could be trusted, it would imply that all possible types of structure are exemplified among existing animals and that any study of fossils is so much time wasted. So far from being able to work in this fashion, the best and most careful workers have been guilty of gross blunders in the determinations which they have made of isolated limbs or feet. An example or two will make this clear.

Some years ago I had the pleasure of visiting Dr. Forsyth Major and examining some of the beautiful material which he had gathered in the island of Samos. In the course of conversation he expressed his conviction that *Chalicotherium* (then known only from skulls) and *Ancylotherium* (known only from

limbs and feet) were one and the same animal. I was utterly incredulous, and, though scoffing at the idea that an animal with a Perissodactyl skull could have feet which such men as Cuvier had declared to be Edentate, I yet was curious to hear the reasoning which had led to such an impossible result. The reasoning was as follows: No one has ever seen the feet of *Chalicotherium*, or the skull or teeth of *Ancylotherium*, yet the two are always associated in the same localities and in the same geological horizons. I admitted the force of these facts, but felt that the structural incongruities involved an insuperable difficulty in the way of the conclusion drawn from the facts. A few months later I was in Paris and saw the fine mammals which Professor Filhol had just excavated at Sansan, among which was a complete skeleton that demonstrated the correctness of Forsyth Major's view; it had the skull of *Chalicotherium* and the feet of *Ancylotherium*.

Quite as remarkable is the case of *Agriochoerus* in this country. The skull was described more than forty years ago by Leidy, and referred to the *Artiodactyla;* many years after a fragmentary fore limb and foot were referred by another observer to the *Carnivora*, while a third referred the hind foot to the *Ancylopoda*. Subsequent discoveries showed that the three supposed genera were one, and that the skull, fore foot, and hind foot, which had been distributed among *three mammalian orders*, all belonged to the same animal; nor was this distribution without good excuse.

Obviously, the guesswork method of restoration must be relegated to the limbo whence it so persistently emerges. In its place we have the plodding, drudging method of finding the bones themselves and not trusting to the imagination for them. Much the most satisfactory way to work is to deal with complete individual skeletons, but it is only comparatively seldom that the observer is so fortunate as to have material of this kind. In the great majority of instances the various imperfect specimens must be combined to make one complete one, and to do this, it rarely suffices simply to put together the various bones of different individuals and make a single specimen out of them, for almost always there is some discrepancy of size or

proportion to prevent such a combination. The way of effecting it is as follows:

Suppose that Specimen I of a given species consists of a skull, vertebral column, and hind limbs, the problem being to supply the missing fore limbs; let us assume further that Specimen II of the same species has the skull, femur, and fore limb. The femur is thus common to both, and we have the proportion (calling the humerus of the second specimen H'', the femur F'', and the femur of the first specimen F') as follows:

$$F'' : H'' : : F' : x. \quad F'' x = H'' F' \therefore$$
$$x = \frac{H'' F'}{F''}$$

If the comparison is made from a few specimens, individual variations in size and proportions are apt to give a more or less grotesque result, but this may be corrected by employing a large number of individuals and making the calculations as often as possible and by the aid of as many different bones as possible, and averaging the result. Such a method is tedious and requires great supplies of material, but it has the advantage of being trustworthy.

In making the figure of a restored or composite skeleton I find the following mode of procedure useful: The most complete individual is laid out in a natural position in a box of sand, and photographed; the photograph is then drawn in outline on a large sheet of bristol board by the aid of the camera lucida, the missing parts are calculated from other specimens and drawn in their proper places, the whole adjusted, and, if necessary, redrawn. It often happens that more or fewer bones are missing from all the specimens, especially the more fragile and loosely connected bones, such as the scapula, ribs, sternum, and caudal vertebrae. These, if not too numerous, are supplied conjecturally, and this fact is indicated by leaving the missing bones unshaded in the drawing. With all due care, however, and with seemingly abundant supplies of material, restorations sometimes go ludicrously astray, and probably none is ever made entirely free from faults. Still, the making of them serves a useful purpose, for I find that even after studying the

separate bones for weeks, measuring, and writing descriptions of them, I am always more or less surprised by the appearance of the skeleton, when the bones are laid together in their natural position; there is always some feature of proportion which had eluded attention.

There is another reason which makes it highly desirable to have a large number of individuals representing each species, and that is the very deceptive effects of even slight crushing and distortion of the bones. So great is the pressure of the overlying weight of sediment, even in undisturbed and horizontal strata, that the bones are frequently somewhat distorted or crushed. No one who has not examined a suite of specimens can understand how totally the appearance of a fossil may be changed by crushing, and the change may be so wrought as to seem normal, except after a very careful examination. Two skulls of the same species, one of which has been compressed laterally and the other vertically, will look so different that at first it seems absurd to refer them to the same animal, and several species, to put it mildly, have been established on characteristics due to this process. To correct the false impressions due to distortion, it is desirable to have many specimens, and, even if none of them is quite symmetrical, a careful comparison of the effects of crushing in different planes will enable the observer to eliminate those effects and to reconstruct the normal form of the species.

A suite of well-preserved specimens from successive geological formations gives the material from which phylogenetic series are to be reconstructed, and if the material is abundant, and the series not interrupted by gaps, the results of careful and conscientious work may be accepted with confidence. Phylogenies, as hitherto made, have usually been confined to genera, which give results too vague for many important purposes; but already an encouraging beginning has been made in constructing phylogenies of species. In the modern way of collecting the exact level of every specimen in the strata is carefully recorded, and thus it becomes possible to trace the successive modifications, even of a species, through a few hundred feet of beds which were uninterruptedly deposited. This

method has long been followed, and with brilliant results, in the case of the Ammonites, but only of late has material been collected in sufficient quantities to make it applicable to mammals.

With all its difficulties and drawbacks, palaeontology possesses certain preëminent advantages over other methods of morphological inquiry. The observer deals, not merely with contemporary forms, whose likenesses or unlikenesses to one another must be arbitrarily valued, nor with embryonic stages whose characters must be interpreted according to the judgment of the individual worker, but with the actual line of descent and in its true order of chronological succession. This is an advantage the importance of which can hardly be overestimated, and one which justifies the expenditure of unlimited time, labor, and money in the work. This it is, more than anything else, which encourages the worker to persevere in spite of every obstacle, content if years of labor result in the full knowledge of a few forms and the identification of a few links in a phyletic chain.

In the investigations which we have so far considered the whole stress has been laid upon morphology, and for their successful prosecution great numbers of finely preserved specimens are required; but there are other lines of inquiry in which very shabby and fragmentary fossils may be of great service. One of these subjects is the fascinating one of the geographical distribution of mammals. It is already possible to analyze the existing North American fauna and point out the indigenous elements derived from a long line of native ancestry, and to identify the immigrants from the Old World and from South America. In many cases we may go so far as to specify the geological date of the migration. Further, we can, in several instances, prove the American origin of certain faunal elements now confined to other continents. For this purpose complete specimens, though desirable, are not indispensable. Genera and species may usually be identified from the teeth alone, and, while phylogenies cannot be safely constructed from such material, the cardinal facts of distribution may be thus determined.

Still another department of investigation may be carried on with the aid of very imperfect material, namely, the correlation of geological horizons in different continents. This is a necessary preliminary to the study of the problems of distribution, in order to determine the place of origin of the group in question. In the present state of knowledge this correlation is difficult, if not impossible, in the case of continents which are and long have been completely separated from each other, and therefore have no common elements in their faunas. It is this fact which makes the correlation of the South American Tertiaries with those of North America and Europe so puzzling. But when the continents have been repeatedly, or for long periods, connected by land bridges, as is true of the land-masses of the Northern Hemisphere, the problem may be attacked with every prospect of success, and many North American formations seem to have their exact equivalents in Europe. To make out these equivalences, it is only necessary that the fossils shall be determinable, generically and specifically.

You have listened with exemplary patience to a dry and dull exposition of methods, but if the listening has convinced you that the methods of modern palaeontological investigation are truly scientific and trustworthy, and that its results are entitled to a respectful hearing on the part of morphologists, I shall not feel that the dullness and dryness stand in need of any apology.

PRINCETON UNIVERSITY.

FIFTH LECTURE.

THE PHYSIOLOGY OF EXCRETION.

ARNOLD GRAF.

Assimilation, respiration, and excretion are essentially cellular processes, that is, they take place within the cell body, and are manifestations of the minute organization of the cell.

Food is, for instance, taken up by the animal, and, after a preliminary mechanical preparation by chewing, transferred into the intestine, where certain substances which are secreted by special elements dissolve the food and thus prepare it for its further fate. We often call the processes taking place in the intestinal tract assimilation. This is logically an inadequate term, because these processes are only the forerunners of true assimilation; they fulfil only the task of making food digestible. True assimilation takes place within the tissue cells, to which the liquefied and chemically transformed food is carried by special elements of the blood. The tissue cells use the food for the regeneration of their protoplasm, which during the life processes of the cells has become partly used up.

The term respiration is widely used to denote the action of breathing, the mere inhalation of air into the lung. This mere pumping of air into the ramifications of the lung is not respiration, although we generally call it thus, but only the preparation to this end. Respiration takes place within the blood corpuscles in the higher animals, in the blood plasm in the lower ones, and is a purely cellular process.[1] If we call the pumping of air into the lungs or the solution of food inside

[1] The intracellular respiration providing the oxygen for the cellular activity coincides, in all probability, with certain phases of metabolism, by which oxygen is set free within the cell.

the intestine respiration and assimilation, we might as well call the crushing of ore in a quartz mill gold or silver production.

Excretion itself is not the mere throwing out of waste products, but it is a complicated cellular process, a task which a certain cell fulfils as an independent unit as well as in intimate correlation with other elements of the body. My attempt is to show the minute mechanism of excretion, and I shall try to make this clear by tracing the paths along which the waste products are carried, by describing the changes which take place during excretion in the cellular elements involved in this process, and by showing how the balance between expended energy and regeneration is continually kept up by the introduction of new structures and new actions in the relative elements.

Cellular metabolism shows the following processes, which, by the way, are so interwoven and gradational in their mutual relations that it is very hard to keep them apart: —

(1) Assimilation, or the transformation of given nutritious substances into bioplasm with the aid of preëxistent bioplasm.

(2) Respiration, or the oxidation of bioplasm, by which the bioplasm is partly transformed into energy, motion, and heat, and partly changed into oxidized materials, — waste products.

(3) The process of excretion, or the discharge of waste products from the cell.

All three (assimilation, or building up; respiration, or transformation; and excretion, or loss) together constitute the cellular activity which is itself the answer to outer stimuli.

The external stimuli and the stimulated cell, or bioplasm, together constitute life; the phenomena of life are stimulus and reaction (cellular activity), and what we call structure is only the path along which reaction follows the stimulus. This I shall briefly attempt to show in this paper, but I have to refer for a more detailed account of my theories to a paper which is being published in Germany entitled *Hirudineenstudien*, and which will possibly appear at the same time as this paper.[1]

[1] A short abstract of these views is contained in my paper on the individuality of the cell (State of New York State Hospitals Bulletin, vol. II, No. 2, 1897), which paper appeared nearly one year after this lecture was delivered.

During the metabolism of the cell waste products (oxidized plasm) are formed, which are expelled from the cell in the form of small granules, concerning the fate of which I have now to speak.

These granules are either discharged into the body cavity or into the vascular spaces, or they remain on the surface of the cell between the connective tissue elements. Their further fate is dependent upon certain cells, the function of which I discovered in these animals, and which I call excretophores. These excretophores are large cells, originating in the endothelium of the body cavity. Certain endothelial cells liberate themselves from the walls of the coelomic cavities, and assume a wandering mode of life. In this state they are comparatively small cells with a distinct oval nucleus and no apparent outer membrane. The protoplasm appears in the living cell to be very finely granular, and the living cell is in a state of continual motion. The cell sends forth pseudopodia, by the aid of which it moves about in the body, and during this wandering accumulates the excretory granules which I have mentioned before.

Part of the excretophores lie in the coelomic cavity; others wander between the tissues, and wherever a foreign particle comes in their way it is picked up and imbedded in the cytoplasm. This picking up of foreign matters is merely a mechanical process which is well known in Amoeba, in the Myxomycetes, and in the leucocytes of the higher Vertebrates. In the latter this process plays an important part in pathology under the name of phagocytosis.

If an Amoeba creeps upon some substratum, it sends forth pseudopodia in one direction, and the main body containing the nucleus follows by the law of cohesion. This motion is not merely an advance in one direction, but it is a complicated vortical motion, as Ryder has shown. We can compare it to a natural stream, where the motion in the middle is quickest, whereas the two sides move slower, this being still more complicated by the fact that the water at the surface moves more rapidly than that at the bottom. In an Amoeba this is even more pronounced than in a stream of water. By this vortical motion all the small particles which adhere to the surface are

drawn into the center of the animal and imbedded in the cytoplasm.

In the same way the excretophores get loaded with excretory granules, and these are further disposed of in the following ways :

The intracoelomic excretophores arrive, after they are well loaded with excretory material, in the neighborhood of the nephrostomes and disintegrate there. Their contents, liquefied plasma, nuclei, and excretory granules, are drawn into the funnel by a ciliary current. From the inner cavity of the funnels the waste products are brought into the adjoining nephridial cells, and being conveyed through the entire length of the nephridium, they finally get to the exterior.

The extracoelomic excretophores wander about between the tissues and pick up the waste products which are discharged from the different elements. A great quantity of waste products is produced by the contents of the small blood-vessels and the capillaries, and we may observe the excretophores gather around these organs and pick up small granules which lie on the surface of the walls of the capillaries. After they are loaded with waste products they begin to wander toward the dorsal surface of the animal, which wandering is due to a positive chemotropism towards oxygen. The dorsal layers of the skin are the seat of capillary respiration, and are therefore to be regarded as a hearth of free oxygen, towards which the excretophores wander.

As soon as these cells arrive below the epidermis, they disintegrate, and their remains constitute the pigment. Our main task is to explain these phenomena, to study the minute mechanism and chemism of excretion.

The first question which we have to answer is: *What changes take place in the excretophores when they pick up excretory granules ?*

Before I can answer this question I have to speak of one property of protoplasm which to my knowledge has never been emphasized, and by the conception of which we may treat a series of seemingly widely different phenomena of cellular life under one common heading. This property I call, in the

absence of a better term, the tendency towards isolation, or, shortly, *isolability* of the bioplasm. This means that bioplasm tries to isolate solid and dry foreign matters, if it comes into contact with such. This end may be attained in different ways. Protozoa, for instance, surround themselves with a thick membrane, if the ditch in which they live dries out. In other cases where small solid particles get into the cytoplasm of the cell, they are surrounded by a fluid which the cytoplasm secretes. In this case we get two different results, depending upon the nature of the foreign particles. If these particles are soluble and nutritive, they are dissolved by the fluid which surrounds them, the secretion of which was in the first instance only a manifestation of the negative sclerotropism of the bioplasm, and the solution is used up for the regeneration of the plasma, a process which we call assimilation. The formation of food vacuoles in Amoeba, Infusoria, Helizoa, etc., is evidently only a consequence of the *tendency towards isolation* from the side of the bioplasm, and it is my conviction that the mechanism of nutrition throughout the organic world is based upon this property of the protoplasm.

If, on the other hand, the foreign particles are not soluble, the fluid drops which are secreted around them serve only to isolate them from the irritable part of the bioplasm, and we might term them isolating vacuoles.

Whoever has watched an Amoeba in life has seen that it contains a surprising quantity of solid particles, and has also seen that most of these particles are surrounded by vacuoles. It is my opinion that the honeycomb structure which Bütschli claims for protoplasm and supports by physico-chemical reasons is only a secondary structure. I do not doubt that in Amoeba (which is his chief subject of investigation) such a structure is present, but I claim that protoplasm does not ordinarily possess this structure. An Amoeba creeps around and becomes crowded with solid foreign particles of all sizes. The greater number of these particles will scarcely exceed a microsome in size. It is very probable that every one of these minute granules is surrounded by a special minute drop of secretion, and thus the cytoplasm must present a vacuolated appearance under a high

magnification. Such an appearance is not to be observed in a stationary somatic cell.

Thus we see that we can, by the introduction of this property of isolation, trace back highly important and seemingly heterogeneous phenomena in cell life to a common cause.

After this digression we may return to the excretophores. The imbedding of foreign particles in the cytoplasm of the excretophores is only the first step in a series of important changes in these cells, which finally terminate in the disintegration of the latter.

Let us suppose that an excretophore has by mere mechanical action imprisoned in its plasm a number of solid excretory particles. The isolability of the plasma will soon become manifest, and these granules will be surrounded by a fluid secretion of the cytoplasm. The waste products, being indigestible and insoluble, the fluid which surrounds them becomes part of a definitive structure of the cell. This fluid may be water or may be something else. I cannot *a priori* decide what the chemical value of the secreted fluid is, because I am not sufficiently familiar with the chemism of bioplasma and know nothing about the chemical constitution of the excretory products. What I have seen is this: In Fig. 1 I have reproduced a living excretophore, which was obtained by teasing out a part of a living animal (Nephelis quadristriata), drawn under a very high magnification (hom. imm. 1.5 mm. comp. oc. 6). In the living cell the cytoplasmic network is not visible, and the nucleus appears only as a light drop surrounded by a highly refractive membrane. I have in this figure made a combination, inasmuch as I have added to the drawing of the living cell the nuclear structure (*n*) and the cytoplasmic threads (*cp*) as they appear in a good preparation. The upper

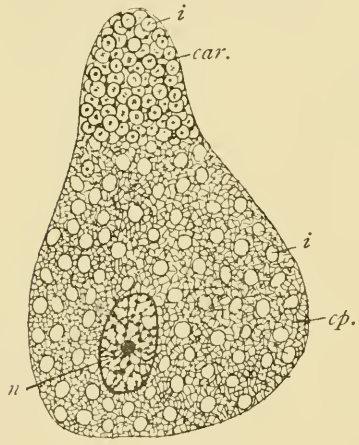


FIG. 1.

part of the figure represents the appearance of the living cell, the lower part that of a stained section.

In the living excretophore we find a great quantity of yellow drops with a dark line around each drop. This is only an optical phenomenon due to the strong refracting index of this substance. Similar black rings surround, *e.g.*, fat drops. In the middle of each drop we notice a number of small, dark granules. In a preparation stained with iron-haematoxylin these drops appear homogeneous and a little irregular in shape, which latter is due to influence of fixing reagents. The cytoplasmic network is very fine and seems to be in some places broken and destroyed. The nucleus shows no features of especial interest. The yellow drops (*i*) are but isolating fluid, secreted around the small excretory granules. I regard this fluid as a mixture of some albuminous substance and some oil or fat acid. This conclusion I am forced to make by the fact that these drops slowly stain brown in the living cell after the addition of osmic acid to the water on the slide. I think that they are only partly composed of oil or fat, because if they consisted of pure oil or pure fat they would darken rapidly with osmic acid, which is not the case. It is apparent that the secretion of these isolating drops must cause great changes in the chemical structure of the cytoplasm, and this consideration will give us a key to answer the next question: *Why do the excretophores wander towards the dorsal surface of the animal after they are crowded with waste products?*

The answer to this question is brief and, in fact, is already contained in the preceding speculations: We have seen that a great amount of the oxygen in the cytoplasm has been used up in the formation of passive structures (the isolating drops), and that in order to keep up its motion and activity the cell has to make up for this loss of oxygen. It is, therefore, necessary for the excretophore to wander towards a place in the organism where free oxygen is continually present.

The dorsal layers of the skin are the seat of capillary respiration in these animals, and in this place fresh oxygen is continually absorbed. This oxygen exercises a chemotropic influence upon the excretophores, which strive to reach the seat of

respiration by wandering toward the dorsal epidermis. Before the excretophores are loaded with waste products the ordinary supply of oxygen is sufficient for their wants, and they only show the above tendency after this ordinary supply is no longer sufficient.

A third question which we have to answer is: *Why do the excretophores disintegrate when they reach the skin?*

We have here to distinguish two successive stages of disintegration, — the mechanical and the chemical. The mechanical disintegration takes place before the excretophores have reached the epidermis; the chemical disintegration sets in as soon as the excretophores have reached the seat of respiration.

We know that during the creeping motion of an Amoeba, or a leucocyte, two mechanical forces act upon the active mass, — the cohesion of the body itself and the adhesion to the substratum. The motion of Amoeba has two phases, active creeping or change of form, and passive reconstruction of form, the progression depending upon these two factors.

I am far from endeavoring to enter into any speculation as to the causes of amoeboid motion, and will only try to show that the two balancing principles of adhesion and cohesion are the cause of the progression and mechanical disintegration of the excretophores.

If an Amoeba creeps, it first sends out a pseudopodium, which adheres firmly to the substratum, and the principle of cohesion in fluids immediately sets in to reconstruct the original form by making the rest of the protoplasm flow after the pseudopodium. The vortical motion depends entirely upon the reciprocal balance between adhesion and cohesion. If we let Amoeba creep upon a substratum, or in a medium where adhesion will overbalance cohesion, the result will consist of a separation of the pseudopodium from the main body, that is, of mechanical disintegration. The moving impetus is given, and of a definite strength, whereas cohesion is not sufficiently powerful to let the body follow as quickly as the pseudopodium advances. Experiments have been made in this line by causing Amoeba to creep in gelatine and the result was a mechanical disintegration of the animal.

This interruption between the proper balance of cohesion and adhesion is similarly the cause of the mechanical disintegration of the excretophores. During their wandering toward the epidermis these cells have to pass through narrow spaces between the muscle-bundles which lie underneath the skin. These spaces are irregular in shape, in some places wide, in others extremely narrow, and we can easily understand that in the narrow places a great resistance is presented to the excretophores. The latter try to overcome this obstacle by sending forth exceedingly fine pseudopodia, which are able to pass through the narrowest spaces, and may enlarge again after they have passed. In the narrowest spaces friction or adhesion must considerably overbalance cohesion, and it is evident that a separation of the pseudopodium from the nucleolated cell body may easily take place there.

These detached pseudopodia will continue to move for some time, and will even reach the epidermis. It is here that the second phase of disintegration takes place, — the final chemical disintegration. The causes of this disintegration are evident. We know that the nucleus exercises chemically a balancing effect upon the substances of the cells. As soon as the nucleus is removed the balance is destroyed and the chemical disintegration sets in.

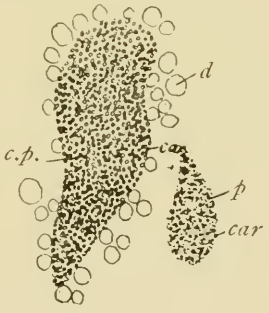


FIG. 2.

Fig. 2 shows in a diagrammatic way the changes which take place in the detached parts of an excretophore. The cytoplasmic (*cp*) network becomes less and less distinct, till finally not a trace of it is left. The isolating drops get gradually smaller and darker in color; at the same time a number of large colorless drops (*d*) are discharged from the remains of the excretophores, and finally there is nothing left but a mass of very small, dark granules (*p*).

It seems to me that as soon as the proper relationship between the substances of the cell is unbalanced a number of noxious substances, as bases, etc., are secreted in the cytoplasmic lymph, which dissolve both the cytoplasmic threadwork

and the isolating drops around the excretory granules, the latter by a soaping process. There are numerous possibilities as to the chemical character of these disintegration products, and it would be a vain attempt for me to go into any further discussion of this matter.

One thing is evident, namely: the excretory granules represent final unalterable products and remain in a solid state after all the other substances in the cell have been dissolved.

The nucleated part of the excretophores which was left behind undergoes a similar fate, but my observations on this point are not so conclusive as those concerning the fate of the pseudopodia. This is mainly due to the fact that in certain stages it is hard to distinguish between parts of the cell possessing a nucleus and those without one. The nucleated cell body continually sends forth pseudopodia, which become detached, and finally very little cytoplasm is left around the nucleus. It seems that the presence of a certain volume of cytoplasm is as necessary for the life of the nucleus as the presence of the latter is for the cytoplasm, because during this gradual loss of surrounding cytoplasm the nucleus gradually loses its normal structure, the chromatin granules cluster together, the membrane disappears and the nuclear network becomes dissolved. Finally, we observe in sections only a dark, homogeneous mass representing the nucleus which it is nearly impossible to detect in the living cell. The remains of the cytoplasm disintegrate in the same way as the pseudopodia, and it is probable that the nucleus also finally breaks up into granules and is carried away in the form of débris by other excretophores.

I have not come to any definite conclusions as to the fate of the dissolved cytoplasm and the colorless drops; it is probable that they consist of nutritive material in fluid form and are absorbed by the surrounding tissues.

Finally, I should like to mention that this whole conception of the origin of the pigment is not only based upon the microscopical study of stained sections and of teased preparations of the living animal, but has also been fully confirmed by experiment. I added to the food of the animals a quantity of fine carmine powder, an absolutely indigestible substance, and tried

to trace the course of the carmine particles within the tissues of the animals. At various periods I made teased preparations of the living tissues, and detected the carmine particles in the excretophores and in their disintegration stages up to the true pigment patches. They are only discernible under very high powers, as they are not larger than microsomes, a fact which makes me think that nutrition and excretion are not merely chemical but also mechanical processes, perhaps rudely comparable to a filtering process. The small black dots in Figs. 1 and 2 represent the carmine particles (*car.*).

We come now to the second part of our task, to the fate of the intra-coelomatic excretophores. The first question we have to answer here is: *Why do the excretophores gather around the nephridial funnels after they have become loaded with waste products?* I have come to the conclusion that the funnel cells of the leeches possess a different chemical constitution from the other nephridial cells, for the following reason: It is a fact that they stain much deeper than the nephridial cells, and that they retain the stain with greater tenacity; indeed, in order to get a good stain of the funnel cells with iron haematoxylin, it is necessary to decolorize the sections until the nephridial cells have become nearly colorless. To what is this due?

It is highly probable that the great activity which the funnel cells possess, the constant contact with substances which are chemically entirely different from cytoplasm, must be the cause of very active metabolic processes within the cells. In this great chemical activity of the cell numerous waste products, both solid and liquid, must be formed and expelled from the cell. I ascribe the great affinity to stains to the presence of such particular waste products. We know that bases will intensify the color of haematoxylin, whereas acids will weaken it. I assume, therefore, a basic nature for these secretions or excretions.

It is a well-known fact that certain micro-organisms possess a strong chemical affinity to certain chemical substances, a phenomenon which we call positive chemotropism. Thus the spermatozoa of ferns exhibit strong positive chemotropism towards malic acid in a certain concentration. If one puts a

weak solution of malic acid into a very fine pipette, and holds this into a dish where fern spermatozoa are swimming, in a short time all the spermatozoa will gather around the end of the pipette, and even enter the latter. If, on the other hand, a strong solution of malic acid is used, the effect is the contrary. All the fern spermatozoa will try to get away as far as possible from the now poisonous substance. If we assume that the basic secretion or waste product of the funnel cells has in a very weak solution a positive chemotropic effect upon the excretophores, it is certain that the cells which come under the influence of the basic fluid will stream towards the point of origin of this substance. In the neighborhood of the funnel the concentration will be greatest, and it is probable, even certain, that the strong base will have a fatal effect upon the cell plasm. The excretophores would retreat if they were not hindered by fresh masses of excretophores pushing forward. In the extreme neighborhood of the funnel the destroying effect of the base now takes place. The cytoplasmic threads are dissolved, the cohesion of the cell is destroyed, the isolating oil drops form soapy substances with the base, and the excretory granules become liberated. I have seen this latter process in the living tissue. Having succeeded by careful dissection in isolating funnels from the body without injuring them, I was enabled to observe them living, their cilia being in rapid motion for hours. (One funnel is about the size of $\frac{1}{5}$ of a millimeter.) During the process of dissection a great number of excretophores were injured and destroyed, and the excretory drops floated freely in the water. As soon as a group of these drops came into close proximity of the funnel I noticed that the individual drops swelled and became transparent, that neighboring drops flowed together and thus formed great colorless drops (*d*), in the middle of which the small excretory granules were suspended. Finally, the drops mixed with the surrounding medium, and the granules (*e*) were freed. This process I have illustrated in Fig. 3.

Before answering the following questions I have a few words to say about the anatomical structure of the funnel and the nephridium. The funnel apparatus consists of two distinct

parts: the crown (*K*), which is formed by a number of ciliated cells, and the receptaculum (*R*), a cavity which is surrounded by a wall of connective tissue and possesses only one opening towards the point of attachment of the ciliated crown cells. This opening is the place where the excretory granules are drawn into the receptaculum. The nephridium consists of a

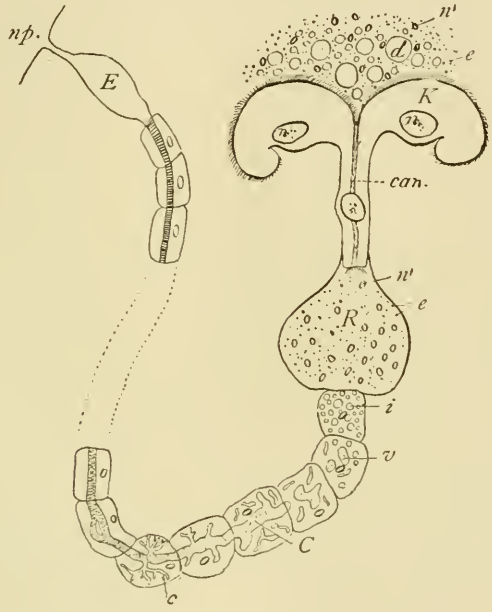


FIG. 3.

row of cells which extends from the receptaculum to the nephridiopore (*np*) or the terminal vesicle (*E*). This is all we need to know for the moment (Fig. 3).

The next question is: *How do the excretory granules get into the funnel cavity?*

I have already mentioned that a current is produced by the cilia which line the free surface of the funnel cells, by which current the remains of the excretophores are drawn into the funnel cavity. I have now to add to this a theory of ciliary motion, which is based upon structural evidence. From the surface of a ciliated cell and slightly inclined to the same arise a great number of parallel straight rods, which stain intensely

blue with haematoxylin, and which are arranged in regular rows. On the outer end of these minute rods (*b*) (which I have called basal rods) are attached small round masses of a light blue staining substance (*m*). All these latter masses are in contact with each other, and it seems to me that this is the most important detail in the whole structure. From the outer ends of these round masses, or, as we might call them, middle pieces, arise the true flagella (*f*), the long thin cilia. Thus a cilium consists of three parts, the basal rod, the middle piece, and the flagellum (Fig. 4). So much for the structure of the cilium proper.

Fig. 4.

The structure of the cell to which these cilia belong is none the less remarkable. We know that in ordinary cells the cytoplasm consists of two distinct substances: a fibrillar substance, which forms a fine threadwork with innumerable meshes, and a fluid which lies between these meshes. In the ciliated cell the fibrillar substance is distributed in a very regular way. There are no meshes to be seen, but all the fibres run parallel to each other and at right angles to the ciliated surface, clear through the whole width of the cell. There are no anastomoses between the fibres (*cp*). They show no relation to the nucleus. On the inner side of the ciliated surface and also around the nucleus we find a great number of fine pale granules (Fig. 5).

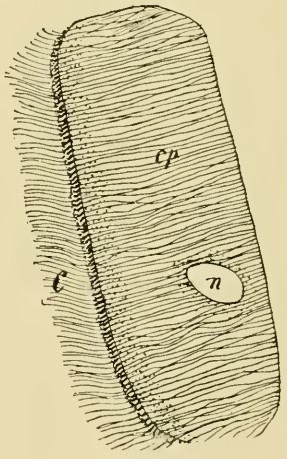


Fig. 5.

Now to our theory. I believe that a stimulus coming from the exterior is necessary to produce the ciliary motion. This stimulus may be a mechanical one, as, for instance, granules striking the ends of the flagella; or, still more probably, a chemical one, for instance, oxygen *in statu nascendi*, which we

know is freed by the above-mentioned soaping process. This stimulus acts upon the flagellum, which transmits it to the middle piece. The middle piece transmits it, changed into impulse, to the basal rod, which contracts and expands rapidly and thereby reacts upon the middle piece, which, being in contact with the neighboring middle pieces, distributes this disturbance over the whole row of middle pieces. I am opposed to the general view that the flagella are contractile, because we never could get any vibratory motion as a result of their contraction, and, moreover, we ought to observe an elongation and shortening of the flagella which has never yet been observed.

If, on the other hand, we accept a rapidly alternating contraction and expansion of the basal rods, the ciliary motion is easily explained. The contraction of the rod drags the flagellum a short distance toward the cell surface, and during the following expansion the flagellum, being elastic, will be bent on account of the resistance of the medium. The fact that the rods are all slightly inclined towards the cell surface explains how the flagella make a stronger inclination to one side. The continuous wave of ciliary motion over a whole ciliated surface is explained by the continuous contact of the middle pieces.

If my theory is true we have here a minute nervous system in one cell: (1) The flagellum, the receiver and conductor of stimuli. (2) The middle piece, a motor centre which transmits the stimuli, changed to impulses, to (3) the contractile rods, which represent the muscular system. The rod contracts and returns a sensational impulse to the middle piece, which distributes it peripherally to the neighboring middle pieces. The middle piece acts here as a centre for the transmission of impulses, both centripetal and centrifugal, which is an extremely simplified mechanism for nervous transmission.

I assume that the stimulus comes from the outside because if it originated in the cell all the rods should contract at the same time and no continuous ciliary wave could result.

This extreme activity means constant use and loss of material and energy. In order to be active an organ has to be well fed and supplied with a certain amount of free oxygen. The

latter is furnished to the cilia by the disintegrating excretophores; the food is constantly carried to the surface of the cell in the form of small, pale granules, which I have mentioned. You perceive how beautifully all the wheels in this process fit together. The cell is active; waste products are formed; these enter into new chemical combinations with the substances in the excretophores. Oxygen is freed by this, and the cell thus obtains, even through the agency of its own waste products, fresh oxygen which stimulates it to continued activity. At the same time the noxious waste products are taken care of and washed into the funnel cavity. The peculiar arrangement of the cytoplasmic threads in the cell is possibly due to the constant mechanical action of the food stream which flows toward the ciliated surface.

I have endeavored to represent these different correlated processes by a diagram, which is indeed extremely schematic and very defective in detail, but which shows my idea of the processes better than any verbal description (Fig. 6).

R represents the receptaculum, the rectangle A the funnel cell body, B the ciliary apparatus on the surface of the latter, and E the approaching excretophore before disintegration.

In A I have given the factors for metabolic activity: $O =$ Oxygen, $P =$ Protoplasma, and $F =$ Food.

Plasma plus oxygen enters upon the process of destructive metabolism, the terminal product of which is a substance ($P-W'$) capable of regeneration, or, better, endowed with reconstructive affinities, and a waste product W'. The food F may by the action of the nuclear substance be divided into, say, two parts F' and F''.

F' enters with $P-W'$ upon the process of constructive metabolism (probably under the influence of the nucleus), the final result of which is the original Plasma P. The fate of the waste product W' is to be considered later on.

In B we have the given factors: $C =$ ciliary substance, and $O =$ oxygen. These two substances affect each other also in the sense of destructive metabolism, the result of which is M, ciliary motion; W'', waste product; and $C-W''$, a reconstructible substance similar to $P-W'$ in A. F'', the second part of

the food in the funnel cell body is carried into B, and reconstructs with C–W'' the original ciliary substance C. The waste product W'' is discharged and carried away into the receptaculum.

In the excretophore E we find the following given factors:

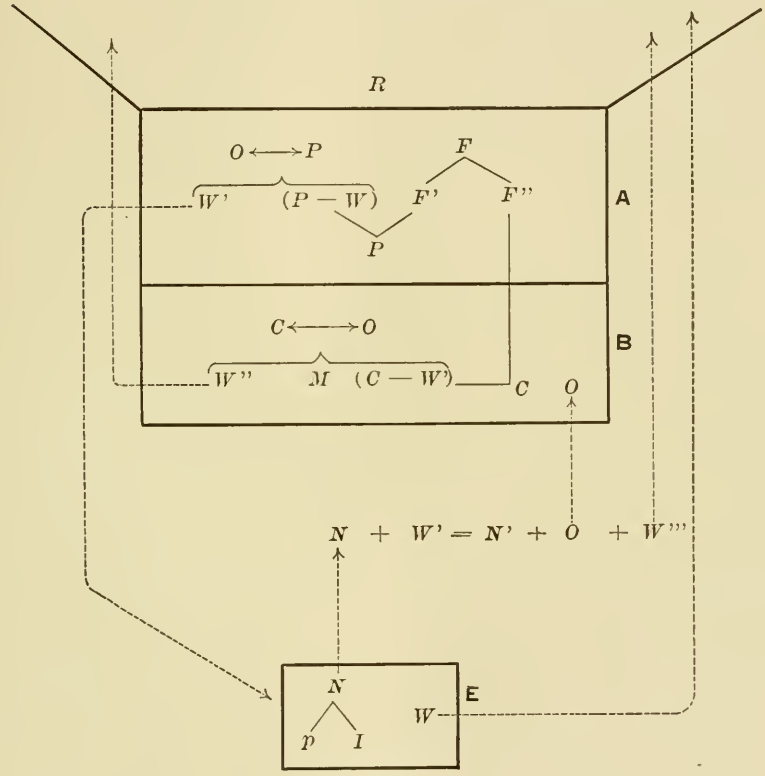


Fig. 6.

W = the excretory granules picked up by the cell during its wandering, and N = nutritious substances composed of plasma P and the often-mentioned isolating drops I. The secretion or waste product W' from the funnel cell body A influences the excretophore E so that the latter disintegrates. During this process W' reacts on N, and as a result of this chemical process we get N' = fluid nutritious substances, which are possibly used up by the surrounding tissues. O = free oxygen, which is

taken up by the ciliary apparatus *B*, and undergoes destructive metabolism with the newly formed ciliary substance *C*; *IV'''*= waste products, which are carried into the receptaculum, and *IV*=free excretory granules, which undergo the same fate. Thus the circle is closed. We find now all the excretory substances assembled in the receptaculum, and it is of interest to know how they get out of this vesicle and into the nephridium. We know that the receptaculum is surrounded by a wall of connective tissue, which is only open at the point of insertion of the crown cells, and there is no perceivable connection with the nephridial cell in the form of a canal or even a break in the wall. It was very difficult for me to imagine a reason for this fact, until lately a very simple explanation occurred to me, which seems quite satisfactory.

We know that the funnel projects with its crown into the coelomic spaces. In the leeches the body cavity is filled with blood, as the coelomic and the vascular system are in open communication with each other. We easily see that, as a stream of blood is carried into the receptaculum by the ciliary motion, if there was an open communication with the nephridial cells it would also be drawn into these and carried to the exterior. This would imply a continuous hemorrhage at every nephridiopore of the animal. This hemorrhage would certainly be highly disadvantageous to the animal, and in order to prevent it the receptaculum is closed. One might oppose to this theory the fact that in numerous other groups we find funnels which are in open communication both with the coelom and the exterior, but in all these cases the body cavity is entirely separated from the vascular system. Thus in the *Oligochaeta*, *Polychaeta*, and *Vertebrata*, no blood can enter the nephridium or the pro- or mesonephros respectively. The receptaculum in the leeches acts as a reservoir, or as a sorting mechanism, into which ever fresh quantities of waste products are brought. The solid particles are unable to get out of the receptaculum, because the cilia of the crown cells form a regular hedge around the only opening of the vesicle. The liquid blood simply overflows and the granules stay within.

The process is to be compared with the throwing of small

pebbles into a vessel full of water. As soon as the vessel is entirely filled with pebbles nearly all the water has overflowed. As to the question how the granules get into the nephridium I have not any definite idea. It is possible that, after the receptaculum is entirely filled with solid waste products, these may effect a stimulus upon the wall of the receptaculum and, with the aid of a chemotropism towards the nephridial cells, might be forced through small spaces between the connective tissue cells of the wall into that neighboring nephridial cell which is in direct contact with the receptaculum. Sometimes the receptaculum even overlaps a great part of this innermost nephridial cell.

This structure of the funnel fulfills the double end, firstly, of preventing nutritive blood from being wasted, and, secondly, of preventing the topmost nephridial cell from being overloaded with foreign matters, to take care of which would be an impossible task for the cell.

The further fate of the excretory granules before they reach the exterior is highly interesting, and can only be determined by a very careful study of the structure of nephridial cells from different parts of the nephridium.

In the following discussion I shall use the term inner cells for those cells of the nephridium which are near the funnel, and outer cells for those which are nearer the nephridiopore.

The structure of the two or three innermost cells of the nephridial row is as follows: The nucleus is very irregular in shape and is surrounded by a thin membrane, which is broken in places. The cytoplasm consists of a beautiful threadwork of very distinct anastomosing threads, round which the microsomes cluster. Besides the cytolymph, we find between the meshes a great number of vacuoles (*v*) in the cytoplasm, and in these vacuoles (which are filled with a watery fluid) we discern small granules, which are no other than the excretory granules. The vacuoles vary considerably in size. Here, again, is a manifestation of the isolability of cytoplasm with regard to foreign solid particles. The cytoplasm is stimulated by these granules and secretes around them an indifferent fluid (Fig. 7). In a number of the following cells we notice new structures which

vary in different genera and even species. In *Nephelis* and some species of *Clepsine* several large vacuoles (*v*) lie in the centre of the cell and even flow together in different places. The periphery of the cell is crowded with smaller vacuoles (*v*), which also flow together in various directions, thus forming an irregular network of canals (Fig. 8). In other species of *Clepsine* (bioculata, nepheloidea, parasita, Hollensis) we notice a very peculiar structure. The centre of the cell is occupied by a dense, irregularly shaped mass (*vm*), which stains deeper than the surrounding cytoplasm. Under a very high magnification this mass shows itself to be composed of innumerable very small vacuoles closely pressed together and with little granules in the centre (Fig. 9). I attribute the deeper stain of this mass to the fact that the cytoplasmic threads are closely wedged in between these vacuoles. In the cells next to these we notice that the vacuoles of this mass flow together in rows and plates, and that even the central masses of two neighboring cells unite (Fig. 10).

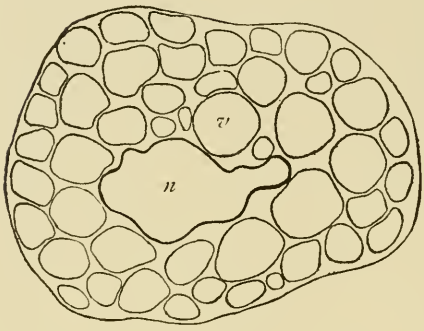


Fig. 7.

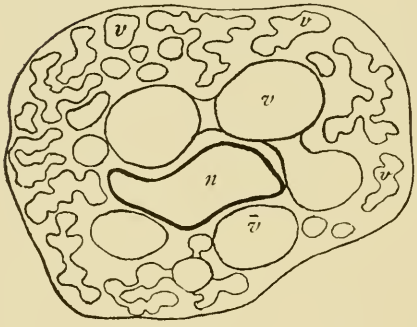


Fig. 8.

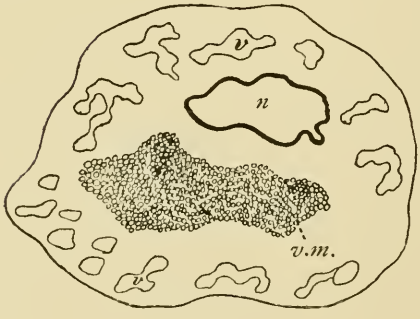


Fig. 9.

This central mass of vacuoles gives origin to one continuous central canal, which runs through the whole length of the following cells and opens into the terminal vesicle. The same is

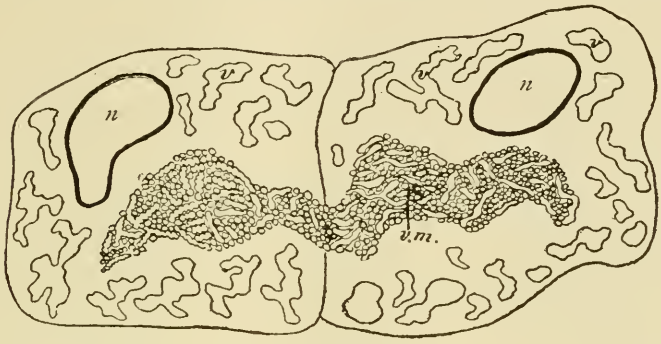


FIG. 10.

the case with the large central vacuoles which I have mentioned as occurring in other species.

The peripheral vacuoles in the next cells flow together (*vc*) and communicate with the central canal (Fig. 11). These side canals finally assume the form of bushes or trees, in which the stem represents the canal of communication with the central canal, from which stem are given off finer and finer branches to the periphery of the cells (Fig. 12, *c*).

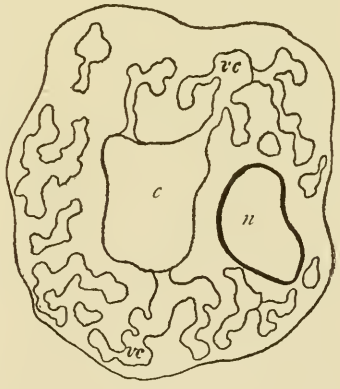


FIG. 11.

As soon as the central canal is formed we notice new organs in these cells. All along the periphery we see, projecting into the interior of the cell, coarse short threads (staining deep red with Bordeaux red), each thread ending in a coarse knob, which stains intensely blue with haematoxylin (Fig. 13, *p*). The cell certainly is in a state of great activity, as is also shown by continual changes taking place within the nucleus. Figs. 14–19 show us nuclei as I have observed them in the upper part of the nephridium. Fig. 14 shows the chro-

matin and other granules evenly distributed through the whole mass of the nucleus. In Fig. 14 a gathering of granules at one point is seen. Fig. 15 shows how perfectly round nucleoli (*nl*) have been formed. In Fig. 16 we notice that in the interior of the nucleolus vacuoles (*v*) are formed, which grow bigger and bigger (Fig. 17), and finally become so large that the solid substance of the nucleolus only appears as a thin membrane, and the nucleolus itself assumes quite fantastic shapes (Fig. 18). Finally the fluid pressure from the interior is so great that the nucleolus bursts and the remains of the membrane are scattered through the nucleus in the form of irregular plates (Fig. 19).

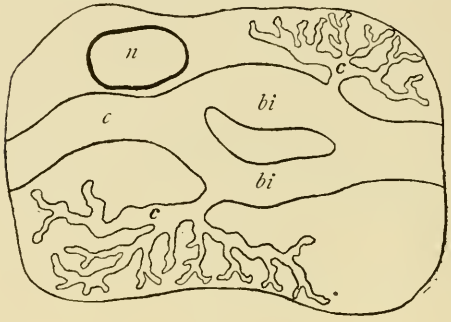


FIG. 12.

This whole process is highly interesting and shows that even in a resting nucleus there is perpetual unrest, not merely chemical but also mechanical activity. The term "resting nucleus" is a very unfortunate one, which ought to be entirely discarded. We might instead of it, perhaps, use the term nucleus alone, without any adjective, which is entirely sufficient.

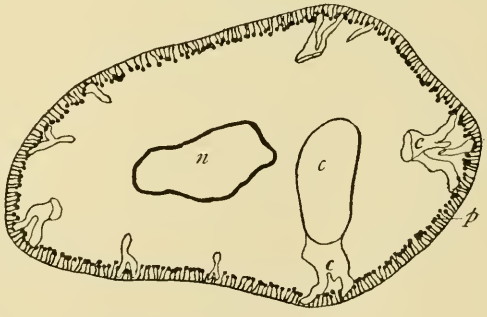


FIG. 13.

The central canal is in the beginning of its formation irregular, and often shows bifurcations (Fig. 12, *bi*); but it soon loses all irregularity, and is in the outer cells of the nephridium a perfectly round tube piercing the cell body. This central canal becomes surrounded by a cuticula which is the seat of a new and highly interesting structure. The side canals are also invested by a fine cuticula.

In a few of the cells following those last described the cuticula of the central canal is reënforced by a network of fibres which is first irregular, but soon assumes a definite arrangement. This arrangement is as follows:

Imbedded in the cuticula we find thick threads which form a perfect ring around the canal and stain deeper than the cytoplasmic threads. These rings are placed at right angles to the axis of the canal and lie at regular short intervals from each other;

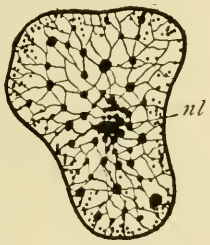
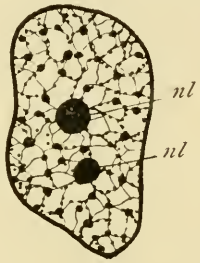


FIG. 14.



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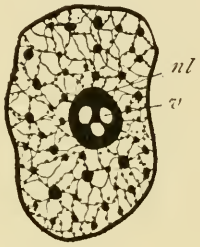

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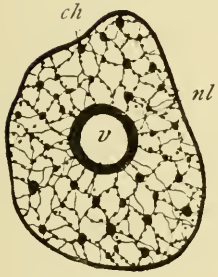

FIG. 17.

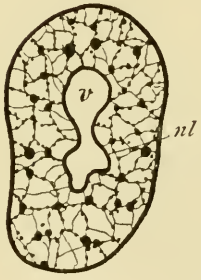

FIG. 18.

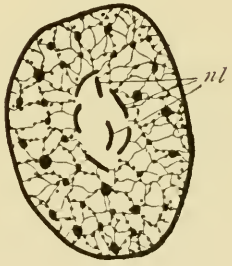

FIG. 19.

they are studded with dark-staining coarse knobs (*k*), which are likewise placed at equal distances from each other. Between the rings there are anastomoses in the form of fine cytoplasmic threads which run from one of these knobs to other knobs of the next ring (Fig. 20, *m*). I have not the least doubt but that this structure represents a musculature of the cell, that the ring fibres are contractile, and that by their contraction a peristalsis ensues, which hastens the discharge of the contents of the canal to the exterior. The side canals have entirely disappeared in these cells, and the muscular structure remains

the same as far as the outermost cell opening into the nephridiopore, or the terminal vesicle. We have now studied the structure of this intracellular canal system, but we ought also to give an explanation of the cause for its formation.

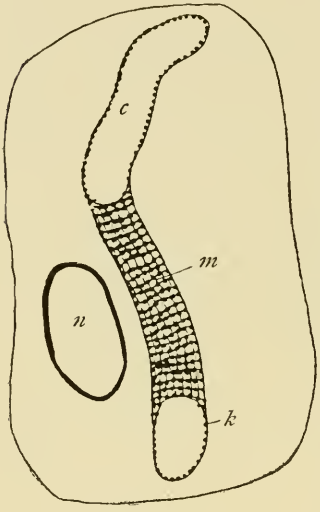

FIG. 20.

In order to gain an idea about the formative cause of these remarkable structures, let us suppose for a while that the receptaculum is connected with the exterior by only one cylindrical cell. On the inner surface of this cell granules will be discharged from the receptaculum and carried into the cell, where they are immediately surrounded by vacuoles (Fig. 21, *i*). These vacuoles will be equally distributed through the whole mass of the cytoplasm, and where the cell surface is exposed to the exterior some of the vacuoles will burst and their contents will be discharged to the outside (Fig. 22, *e*). The cell is thus partly released from excretory products, but new granules are continually taken up at the inner surface and isolated by fluids, and new vacuoles are emptied at the outer surface. We clearly see that there is thus a continual push coming from the inner surface, and a pull, so to speak, coming from the exterior. These forces produce in the liquid contents of the cell a continuous stream towards the exterior. It is evident that the celerity of this stream is greatest near the outer surface of the cell, because the friction is least and there is hardly any resistance. This point of least friction is, therefore, to be considered as a force centre, from which a leading direction is given to the streaming fluids, the

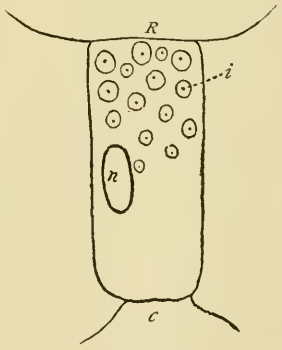

FIG. 21.

same as the centre of gravitation gives direction to moving particles. As a result of this we find the formation of a single canal in the outer part of the cell, into which a number of side canals (*c*) open radially (Fig. 23). In the innermost part of the cell we find isolated vacuoles, because new granules are continually taken up and isolated. These vacuoles flow together in different directions, and only in the lower part of the cell a regular arrangement takes place.

Let us now suppose that this cell divides into two, three, or more daughter cells, and we shall get a structure similar to that of a row of adult nephridial cells. The innermost cells (*i*)

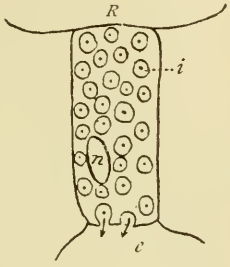

FIG. 22.

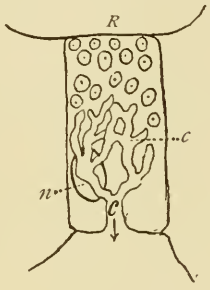

FIG. 23.

are vacuolated, the next pierced by irregular canals (*c*), the next with radial side canals (*c*), and the outer cells with a single central canal (Fig. 3). Let us go a step further. We know that every stimulus is, from the side of the bioplasm, followed by a reaction. The more intense the stimulus, the more energetic the reaction. We easily see that the excretory granules within the isolating vacuoles cannot effect any appreciable stimulus upon the surrounding cytoplasm, but the case is quite different where these vacuoles flow together and form a system of canals, within which a continuous stream of fluid flows. This stream is quickest near the outer opening of the cell, and granules will be thrown against the surrounding cytoplasm and stimulate it. This is exactly similar to what happens in a river. The erosion by the river works continually upwards, thus forming valleys, mountain gorges, and passes. A slow, irregular stream of fluid flows in the anastomosing, irregular vacuole canals. The

granules suspended in this stream will lightly graze the surrounding protoplasm, a stimulus sufficient for the secretion of a cuticula. Where the stream is quicker the friction is greater, and meshes of cytoplasmic threads are formed in the cuticula for a reënforcement. Near the outer opening the stream is very rapid, and here the cytoplasmic threads are regularly arranged in rings and transformed into contractile substances,

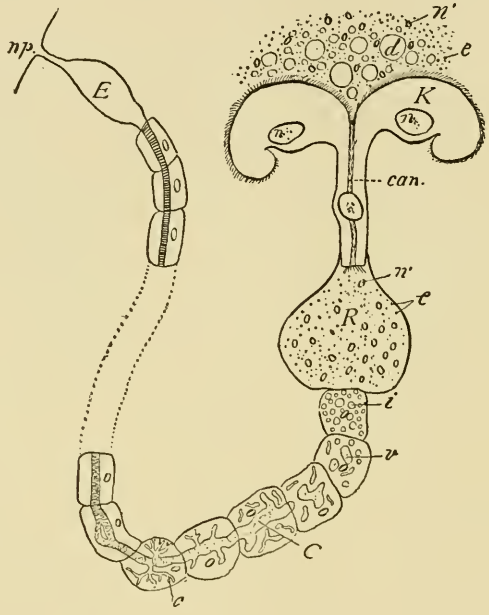

FIG. 3.

rings which contract as soon as a granule floating in the canal is hurled against them. This contraction only accelerates the stream, and thus we understand that this muscular structure also progresses from the outer cells inwards. The thick granules which stud the rings I regard as the direct receivers and transmittors of the stimuli, the anastomosing threads as the sensory conductors, facilitating by their activity a coördinated peristalsis. By the aid of this complicated mechanism within the nephridial cells, the excretory granules are finally discharged from the body. It is evident that these excretory granules are not the only waste products, but that the fluid contained in the

canal system is also useless matter which the nephridial cells secrete and empty to the outside together with the excretory granules.

There is only one more point to speak of, namely, the significance of the peripheral organs (Fig. 13). We must consider that the nephridial cell has an extremely complex function. It has to respire, to assimilate and regenerate its protoplasm, and to discharge the excretory products which are formed during its own metabolism, like any other cell. In addition to these functions, the cell has to secrete isolating substances around the excretory granules, has to provide a mechanism for the discharge of these substances, and has to nourish and regenerate this mechanism. Finally, it has to provide fresh oxygen for the sustenance of the peristaltic motion of this mechanism. I think it possible that the peripheral organs may have something to do with the provision of fresh oxygen; that they are, perhaps, the means of communication between the cell and the surrounding tissues, stimulating the latter to give up oxygen for the benefit of the nephridial cell. I present this merely as a suggestion, not being able at the present time to form even a definite hypothesis as to the purpose of these remarkable organs.[1]

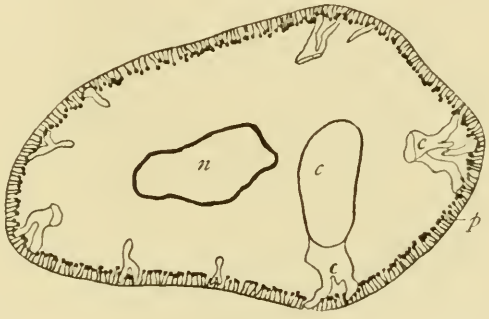

FIG. 13.

We have now completed our task, having followed the paths along which the excretory products are carried until they are thrown out of the body, and also having studied all the changes

[1] During the winter following the delivery of this lecture, I succeeded in finding similar peripheral organs in the ciliated funnel cells of the leeches, and in the intestine cells of the same animals (which are likewise ciliated) and I have come to the firm conviction that these specialized microsomes are the producers of an oxidizing ferment (which ferment exists as we know) by which assumption the last link in our metabolic circle is found. More about this point will be published in another place.

which occur during their discharge and the structures connected therewith. It is evident that all this also has bearings upon our conception of the purpose and meaning of the cell — upon the cell theory in general. This is not the place to deal with the applications which I have made elsewhere of these facts with reference to the cellular theory, and I will only state one point which stands out clearly above the rest.

The cell is a whole. It is an organism both irritable and responsive, and in a way creative. Not only the germ cell, but also the finally differentiated cell must be regarded as an entire organism, which under certain stimuli is able to set free a certain amount of energy and create new structures. The structures themselves are not to be confounded with what we call response to stimulus; they are only a side product during the process of irritation and reaction. Thus the stimulus of a foreign solid particle imbedded in the cytoplasm calls forth the response of secretion. That this secretion assumes the form of drops around the excretory granules is merely due to the physical properties of fluids; this form or structure of round drops is only an expression of the most suitable and direct path along which the response follows the stimulus. Another point which I must insist upon is that structures always appear first where stimulus and protoplasm meet, — therefore, near the surface of the cell. The intracellular musculature around the central canal apparently lies in the interior of the cell, but if we consider that the canal is filled with fluid it becomes evident that, for the cytoplasm, the central canal is as much exterior as the surrounding tissues; that the wall of the canal is an *inner surface* of the cell. The cilia and the peripheral organs appear on the surface of the cell.

There is given, on the one hand, irritable protoplasm, on the other hand, chemical and mechanical stimuli, and, behold! structure has followed naturally. This looks very nice, but we must not overlook the fact that all this only means the surveying and describing of the paths along which phenomena take place, and not an insight into the nature of the phenomena themselves. The cause of life is the same as the one which makes water get firm under a low temperature, and which makes salts

crystallize in regular systems. We do not know why; yet we must abstain from introducing teleological factors into the science of life, because science has to work with given and comprehensible factors, and has to conform to the nature of our own intellect, which is unable to form any adequate teleological conception. If we try to soar above the limits which nature has put to the faculties of our brain, we might as well give up research, cross our arms, and say Credo, or else yearn for Nirvana.

SIXTH LECTURE.

SOME NEURAL TERMS.[1]

BURT G. WILDER.

FIVE conditions have led to the preparation of this lecture.

1. The American Neurological Association, at its session in Philadelphia, June 5, 1896, unanimously adopted the Report of the Committee on Neuronymy embodying the previous reports of three other American committees and extending the list of Latin terms recommended from eleven to forty; see p. 126.

2. The Anatomische Gesellschaft, at its session in Basel, April 19, 1895, adopted the Report of its Committee on Anatomische Nomenclatur comprising a list of Latin names for all the visible parts of the human body, and provided for its revision at intervals of three years. Presumably, the Gesellschaft sanctioned the declarations of principles which had been pub-

[1] Delivered August 3, 1896. A fuller discussion of the subject occurs in the article "Neural Terms, International and National," *Journal of Comparative Neurology*, VI, December, 1896, pp. 216-352, including seven tables. That article comprises nine parts as follows:

I. Definitions of certain terms employed in the discussion of Anatomic Nomenclature. II. Stages of the writer's terminologic progress. III. Report of the Committee on Neuronymy of the American Neurological Association, with commentaries. IV. Discussion of the differences between certain terms in that report and those adopted by the Anatomische Gesellschaft. V. Reply to criticisms offered by the Anatomische Gesellschaft and by its members. VI. Correspondence with Prof. Wilhelm His. VII. List of the neural terms adopted by the Anatomische Gesellschaft and of those now preferred by the writer. VIII. Concluding remarks. IX. Bibliography.

Parts VII–IX have also been reprinted under the title "List of Neural Terms, with Comments and Bibliography." Copies of the entire article or of the "List" may be obtained from Henry Cowell, McGraw Hall, Ithaca, N.Y.

lished by the secretary of the committee (Krause, '91, '94).[1] The list was published early in the summer of 1895 as a part of an article, "Die Anatomische Nomenclatur," by Prof. Wilhelm His, constituting a "Supplement-Band" to the "Anatomische Abtheilung" of the *Archiv für Anatomie und Physiologie*. Certain principles and certain portions of the list merit high commendation; others, in my opinion, are to be as deeply regretted. Among the least acceptable features are the designations and coördination of the encephalic segments and the assignment of parts thereto; see p. 158.

3. In the official action of the Gesellschaft and in a recent manual by the president of its committee, Professor Albert von Kölliker, are declarations against the efforts of the American committees which may be due in part to ignorance or misapprehension of the facts. As chairman of two of the American committees and as secretary of a third, I may not inappropriately endeavor to remove the impediments to a clearer comprehension of our position. I particularly desire to free the committees, their individual members, and the associations which they represent, from responsibilities not yet assumed by them.

4. In the article above mentioned Professor His not only evinces a failure to comprehend the aims of the American committees, but also misrepresents what has been done by me as an individual. Such misrepresentations, unless corrected, might well, especially in Germany, impair the efficiency of my past and present utterances upon Anatomic Nomenclature. A correspondence begun in December, 1895, has failed to adjust our disagreement, and it is most reluctantly submitted to other anatomists. In an experience of thirty-five years this is my first scientific controversy, and I trust it may be the last.

5. During the quarter of a century since my attention was first drawn to the defects of current anatomic terms my convictions may be assigned to five different stages, dating respectively from 1871, 1880, 1884, 1889, and 1895. Beyond the

[1] These numbers indicate the years of publication. The Bibliography would have occupied undue space in the present volume, but may be found by those interested in the papers named in note 1.

last I now discern no opportunity for progress excepting in the elaboration of details. It is my desire to devote the rest of my life to the study of the brain, and this seems to be a fitting time for submitting such statements of principle and suggestions of practice as may facilitate the labors of others upon Anatomic Nomenclature.

The following definitions of course apply to the Latin forms of the English words; the adjectives and other derivatives are self-explanatory.[1]

Onym. — From ὄνυμα, same as ὄνομα, a name. Proposed by Coues (84) in the sense of biologic name. It is seldom needed alone, but is the essential element or base (p. 112) of many derivatives.

Toponym. — From *onym* and τόπος, place. A term indicating location or direction: *e.g.*, *lateral*, at the side; *laterad*, toward the side; *transection*, cutting across.

Organonym. — The name of a part or organ; *e.g.*, *humerus*.

Neuronym. — The name of a part of the nervous system.

Polyonym. — A name consisting of more than one word; *e.g.*, *fissura centralis, rostrum corporis callosi, plexus chorioidea ventriculi quarti, iter a tertio ad quartum ventriculum*. This use of the word *polyonym* is analogous to that of *polyandry*, *polygamy*, etc.

Dionym. — A term consisting of two words; *e.g.*, *vertebra thoracalis, arteria brachialis, gyrus callosalis*. Dionyms are perhaps the most common kind of polyonyms. They have a certain analogy with the technical names of animals and plants, since the noun often indicates a group of similar or related parts and the adjective designates a specific member of the group.

Trionym. — A term consisting of three words; *e.g.*, *vertebra thoracalis prima*. Here, as with the so-called trinomials of zoölogy, the second adjective may be said to designate a subspecies.

Mononym. — A name consisting of a single word; *e.g.*, *insula*. Strictly speaking, a mononym is either a noun or

[1] Definitions may be found also in the more recent English and medical dictionaries.

some other word used as a noun. But the application may be conveniently extended, as in the next definition.

Mononymic Qualifier. — A qualifying word (adjective, participle, or genitive) consisting of a single word; *e.g.*, the second word in each of the following dionyms: *Gyrus postcentralis* (for *G. centralis posterior*), *G. subfrontalis* (for *G. frontalis inferior*).

Ordinal Names. — These indicate the order or numeric location of a member of a series; *e.g.*, *costa prima*, *vertebra thoracalis prima*.[1]

Attributive Names. — These refer, at least in part, to some real or fancied attribute; *e.g.*, *callosum*, *oblongata*, *vagus*.

Simile Names. — These express real or fancied resemblances to other objects by means of the suffixes *formis* or *oides*; *e.g.*, *restiformis*, *trapezoides*. Most simile names might as well be converted into the corresponding metaphoric names; *e.g.*, *restis*, *trapezium*.

Metaphoric Names. — The names of non-anatomic objects are transferred to parts having some real or fancied resemblance thereto; *e.g.*, *pons*, *insula*, *thalamus*, *falx*.

Metaphoric Diminutives. — Since many parts are smaller than the more familiar objects whose names have been transferred to them, the diminutive form is sometimes used; *e.g.*, *vallicula* (from *vallis*), *fasciculus* (from *fascis*), *colliculus* (from *collis*), *clavicula* (from *clavis*). Since, however, size is so variable and unessential an attribute, and since verbal diminutives are commonly longer than their originals, the latter might as well be employed. But this suggestion would not apply to a case where there are two of a general sort differing mainly in size; *e.g.*, *cerebrum* and *cerebellum*; *falx* (*falx cerebri*), *falcula* (*falx cerebelli*).

Polychrestic Word. — One that does duty in many connections; *e.g.*, *occipitalis*, which in various combinations aids in designating at least twenty-five different parts.

Homonym. — A name applied to two or more different parts; an ambiguous term. An extreme case is that of *os* as signifying

[1] With any series extending lengthwise of the vertebrate body the member nearest the head is regarded as first. The only instance known to me of disregard of this conventional assignment is the enumeration of the segments of the brain in the schema of Professor His, as adopted by the German Committee.

either a bone or an orifice; the oblique cases and derivatives of course distinguish them. *Medulla* has been applied to several parts. *Epiphysis* may designate the end of a bone or a part of the brain. Theoretically objectionable, the context commonly frees homonyms from serious ambiguity.

Idionym. — A word which, at least in anatomy, refers to but one part; *e.g.*, *cerebellum*, *thalamus*, *chiasma*, *pons*, *insula*.

Idionyms by Recombination. — *Cornu posterius*, as employed by most anatomists, is a homonym, designating either a cavity of the cerebrum or a feature of the myel (spinal cord). But *postcornu*, as introduced by me in 1881, applies only to the cerebral cavity, and is thus an idionym.

Contextual Explicitness. — For want of a better phrase, this may refer to the possibility of employing terms that might be ambiguous but for their association with others. A common example is *cord*, which may be used in at least five senses, by the neurologist, the laryngologist, the surgeon, the obstetrician, and the embryologist. When an entire publication or section of it refers to a group of organs of the same general character, then the generic element of their polyonymic designations may be often omitted and the specific alone employed; *e.g.*, with arteries, fissures, gyres, etc. Indeed, to be absolutely explicit or idionymic in all cases would require many new names or the addition of genitives or other qualifiers to many already existing.

Locative Names. — The location of a part is a general and comprehensive attribute and, as remarked by Owen, "signifies its totality without calling prominently to mind any one particular quality, which is thereby apt to be deemed, undeservedly, more essential than the rest."

Prepositional Locatives. — With these the qualifying prefix, a preposition or adverb, indicates the location of a part relatively to some other part, more important, more easily recognized, or earlier designated. *Praecuneus* designates a cortical area just "in front of" the cuneus.

Adjectival Locatives. — These indicate either the location of a part within some general region or its membership of a series. *Vertebra thoracalis* designates a spinal segment in the thorax. *Commissura anterior*, *cm. media*, and *cm. posterior*

distinguish members of a conventional series. *Mesencephalon*, *prosencephalon*, and *metencephalon* designate members of a natural series, and the prepositions have the force of adjectives; see pp. 144–150.

Base (*verbum basale*). — The original or more essential element of a derivative, as distinguished from prefixes, suffixes, inflective terminations, etc.

Derivative. — A word derived or formed either immediately or remotely from another; *e.g.*, *inorganic*, *organize*, and *organs* are derivatives of *organ*.

Correlative Names. — These are derivatives containing no obvious locative element, but intended to indicate some relation between the part so designated and the part designated by the base; *e.g.*, *fissura calcarina* indicates the collocation of an ectal fissure with the calcar, an ental ridge.

Eponyms. — Personal names, that is, derived from the names of individuals; *e.g.*, *fissura Sylvii*, *pons Varolii*. These were discarded by me in 1880, and as they are condemned by the German committee most of them will probably disappear. An exception, perhaps, should be *fissura Sylvii* (p. 000).

Pecilonymy.[1] — Proposed by me in 1889 as a mononym for *terminologic variety* or *inconsistency* within a single article or work; *e.g.*, the use of *fissura* and *sulcus* for the same cerebral furrow ; of *centralis* and *Rolando* for the same fissure. Between pages 464 and 507 of Schwalbe's "Neurologie" occur *Crus fornicis* (498), *Fornix-schenkel* (464), *Fornix-säulchen* (507), *Gewölbe-schenkel* (464). His ('95) adopts *Foramen interventriculare*, but uses *Foramen Monroi* on page 166, and "*Monro'schen Loche*" on page 167.

Direct Pecilonymy. — In the cases mentioned above, and others that might be adduced from nearly every work known to me, one and the same part is designated by two or more substantives, or words used substantively. This is *direct pecilonymy*. A special variety of it occurs when different generic names are applied to two homologous parts; *e.g.*, in

[1] From ποικίλος, various, changeful, inconstant; compare ποικιλόβουλος, of changeful counsel; *pecilopoda*, various footed. The unfamiliar term is perhaps the less objectionable in that it stands for a habit which may ere long be eradicated.

Huxley and Hawkins' *Comparative Osteology* the arm is called the "anterior *extremity*, the leg the "hind *limb*."

Indirect Pecilonymy. — But when a certain substantive is used in one passage, and in another an adjective or other derivative from a different substantive, the pecilonymy is indirect or implied; *e.g.*, "certain fibers are called *peduncular* because they pass into the *crura* cerebri." Very commonly a certain fissure is named *Rolando*, but adjoining gyres *paracentral*, *anterior central*, etc.

Pecilonymy by Permutation. — When a name, or the adjective part of a name, contains two or more elements of approximately equal value, they are subject to accidental or intentional transpositions that may cause misapprehension. For example, in his paper on the brain of *Ateles* (*Zoöl. Soc. Proc.*, 1861), Huxley refers to the same fissure as occipito-temporal on page 258 and as temporo-occipital on page 260. One might infer that two different things were indicated, just as, in chemistry, *hydro-carbon* and *carbo-hydrate* have different significations. Similar diversity of usage exists with regard to the occipital fissure, which is called by some *occipito-parietal* and by others *parieto-occipital*. *Orbito-frontal* and *fronto-orbital* constitute another instance.

Abbreviational Pecilonymy. — The following is a good example of a bad system: in the translations of two of Meynert's works occur *corpus quadrigeminum*, *corp. quadrigeminum*, *corp. quadrigem.*, *corp. quadrig.*, *corp. quad.*

The Perpetration or Toleration of Pecilonymy may be ascribed to five mental conditions:

(*a*) Pure heedlessness.

(*b*) Indifference to the just claims of readers and especially of students.

(*c*) Pride in the hardly gained familiarity with the synonymy of parts.

(*d*) Desire to avoid repetition, as in certain forms of literary expression; see W. & G. ('89), § 73, B, note.

(*e*) Unwillingness to commit oneself to a particular[1] name.

[1] In some cases all the current titles of a part are so unacceptable that one recalls Shakespeare's epigram as to the "Small choice among rotten apples," and the demand of the dissatisfied guest, "If this is tea, bring me coffee; if it is coffee, bring me tea."

Such hesitation constitutes the only valid justification of pecilonymy. But the same end might be gained by a simple declaration, without the risk of confusing or misleading the reader.

Magnilogy. — The employment of lengthy or ponderous terms when briefer would suffice. This is simply one form of what may be called *anatomic esotery*. Now that the choice is offered, the anatomist who deliberately says *aponeurosis* for *fascia*, *anfractuosity* for *fissure*, and *convolution* for *gyre*, thereby arrays himself with the village orator, in whose turgid discourse a fire is always a conflagration.

Perissology. — The following example of needless amplification occurs in a special article by a distinguished neurologist in a leading metropolitan medical journal : " The anterior column of gray matter extends throughout the spinal cord, and the upper enlarged intracranial end of the spinal cord, which is known as the oblong cord or medulla (medulla oblongata)." As shown in W. & G. ('89), 529, § 76, the information contained in these thirty-two words might have been given in fifteen.

Equivalents, Synonyms, and Isonyms. — Equivalents are terms meaning the same thing, *e.g.*, *pons*, *pons Varolii*, *pont*, and *Brücke*. Strictly speaking, *pons Varolii* is a synonym, or equivalent in the same language, while *pont* and *Brücke* are isonyms or equivalents in other languages. But for simplicity all may be here regarded as synonyms, just as, in biology, *synonymy* embraces all the appellations of organisms, whatever their nationality. Hence one may recognize two groups of synonyms, *viz.*, *paronyms* and *heteronyms*.

Paronyms and Heteronyms. — Excluding *pons Varolii* (the dionymic, eponymic synonym of *pons*), the other equivalents are the French *pont*, the Italian *ponte*, the Spanish *puente*, the German *Brücke*, and the English *bridge*. Of these the first three are obviously related to the Latin *pons*, while the last two have no such relationship. The former have been called by me paronyms,[1] the latter, heteronyms. A familiar illustration is the Latin *canalis*, of which *canal* is the English paronym, while heteronyms are *tube*, *passage*, *trough*, and *water-course*.

[1] *Paronymy* or paronymization includes what has been called word-adoption, word-appropriation, word-assumption, word-borrowing, etc.

The Greek ὄργανον might be rendered by *part*, *instrument*, or *agent*, and these are its English heteronyms; but the Latin paronym is *organum;* the French, *organe;* the Italian, *organo;* the English, *organ;* and the German, *Organ.* Each of these is, so to speak, a geographic variety of the original or antecedent word; indeed, it may be regarded as the same word modified in accordance with the genius of each language. The case may be compared with that of a traveler who maintains his essential identity notwithstanding "in Rome he does as the Romans do," and in other countries conforms to the customs of the inhabitants in respect to garb and demeanor.

Methods of Paronymization. — For linguistic reasons paronymy is general and easy with the Romance languages, less so with the Germanic and with English. Still, there are examples enough to warrant the belief that into either may be adopted any Latin substantive or adjective.[1] Paronymic methods vary with the language and with the word, and involve more or less orthographic modification, ranging in extent from the case of *fiber* (from *fibra*) to that of *alms* (from *eleemosyna*). These are *changed paronyms.*

Unchanged Paronyms. — But there are other evidences of paronymization, *viz.*, (*a*) Pronunciation; *e.g.*, *Paris*, *Detroit.* (*b*) Hyphenation with a word unmistakably of another language; *e.g.*, in *Balken-splenium*, the hyphen indicates the adoption of the Latin *splenium* as a German word. (*c*) Combination; *e.g.*, *Ponsfasern* and numerous similar terms. (*d*) Declaration that the writer regards the unmodified word as adopted.[2] (*e*) Employment of the vernacular form of the plural or of an oblique case; *e.g.*, the Latin plural of *lens* is *lentes*, but the English is *lenses;* so *atlas* (*atlantes*), *atlases;* *enema* (*enemata*), *enemas;* *animal* (*animalia*), *animals:* in the phrase "fibers of the callosum," the last word might still be regarded as Latin; but if one said "callosum's fibers," the English possessive would indicate paronymization.

[1] Also other and perhaps all parts of speech, but they do not concern us here.

[2] Were all foreign words italicized, then in a given case the non-italicization of a word would indicate its adoption. Since the Germans commonly capitalize all nouns, that feature does not necessarily signify that a word is regarded as an unchanged paronym.

International and National Terms. — By general consent Latin constitutes a common or international language for scientists. National terms may be either unrelated to the Latin antecedents,[1] hence *heteronyms*, or obviously related thereto, hence *paronyms*. *Sea horse*, *cheval marin*, and *Seepferd* are synonyms, but to either an Englishman, a Frenchman, or a German, two of them are foreign words and unacceptable. *Hippocampus* is distinctly a Latin word, and the frequent occurrence of such imparts a pedantic character to either discourse or printed page. *Hippocamp*, *hippocampe*, *hippocampo*, and *Hippokamp* are as distinctly national forms of the common international antecedent (not to invoke the original Greek ἱππόκαμπος), and are readily recognized by all, while yet conforming to the "genius" of each language.

The Paronymic Advantages of Mononyms. — The object of paronymy is to endow anatomic language with nationality without obscuring its internationality. With mononyms the paronymic changes (if any) are slight, involving mostly the termination, or, with German, the capitalization of nouns and the occasional replacement of *c* by *k*. The word is readily recognized, and its abbreviation would be the same in any language. But with polyonyms the relative position of the substantive and the qualifier is commonly reversed in the two groups of languages, Romaniform and Germaniform. In the former the noun more often precedes, in the latter it almost always follows.[2] Hence there is a different aspect of the entire term, and the abbreviations are transposed. The Anglo-paronym of *commissura posterior* is *posterior commissure*, and the respective abbreviations might be *c. p.* and *p. c.*; but if the Latin dionym be mononymized into *postcommissura*, the English paronym is *postcommissure*, and the abbreviation *pc.* answers for both.

Limitations to Paronymy. — As already admitted with regard to mononymy, the "nature of things" forbids the rigid and universal application of the principle of paronymy. Certain parts, so exposed or so vital as to have gained early and popu-

[1] Or related so remotely that the connection is obscure.

[2] Notwithstanding the familiar exceptions, *alma mater*, *pia mater*, and *notary public*.

lar attention, have received vernacular names or heteronyms which are brief and generally understood. Such are *head, hand, foot, heart,* and *brain.* Indeed, the use of the Latin equivalent for either of these would impress most persons as pedantic. But this concession of, for example, the sufficiency of *brain* instead of *encephalon* does not warrant the retention or formation of an indefinite number of inflectives, derivatives, and compounds from the heteronym. The same remark applies to other languages.[1]

The following summary of the changes of my views during a quarter of a century shows, I trust, a general advance in the comprehension of the subject, and justifies me in commenting upon the labors of others.

I. 1871–79. In an effort to confirm, extend, and modify certain morphologic ideas of my teacher, Jeffries Wyman, I enumerated ('71, 172) the following requirements of technical terms: (1) Classic Derivation. (2) Capacity for Inflection. (3) Brevity. (4) Independence of Context for Signification. (5) Non-ambiguity to the Ear as well as to the Eye. (6) Previous Use in a Kindred Sense.

Then, as now, the most desirable (yet not absolutely essential) attributes of technical terms seemed to me (1) Classic Derivation, (2) Capacity for Inflection. But both these had been adumbrated long before by Barclay ('03) and Whewell ('40), and distinctly enunciated by Owen ('46, 171) in the immortal paragraph wherein *myelon* was proposed :

"The fore part of the neural axis . . . is called the brain or encephalon; the rest I term *myelon* (Greek μυελός, marrow). As an apology for proposing a name capable of being inflected adjectively, for a most important part [see W. & G. ('89), § 48] of the body which has hitherto received none, I may observe that, so long as the brief definitions 'marrow of the spine,' 'chord of the spine,' are substituted for a proper name, all propositions respecting it must continue to be periphrastic, *e.g.*,

[1] Of the two German vernacles for encephalon, *Gehirn* is more commonly used alone and *Hirn* in composition. On my list there are 35 compounds of *Gehirn* and 106 of *Hirn;* moreover, of the former, one-half are duplicated among the latter.

'diseases of the spinal marrow,' 'functions of the spinal chord,' instead of 'myelonal[myelic]'[1] diseases, 'myelonal' functions; or if the pathologist speaks of 'spinal disease,' meaning disease of the spinal marrow, he is liable to be misunderstood as referring to the disease of the spinal or vertebral column. But were the anatomist to speak of the canal in the spinal marrow of fishes as the 'myelonal canal,' he would at once distinguish it from the canal of the spinal column. The generally accepted term 'chorda' or 'chorda dorsalis,' for the embryonic gelatinous basis of the spine, adds another source of confusion likely to arise from the use of the term 'spinal chord' applied to the myelon, or albuminous contents of the spinal canal."[2]

In 1873 ('73, 306) Owen's examples of *ectogluteus*, *mesogluteus*, and *entogluteus* led me to propose the locative mononyms *ectopectoralis* and *entopectoralis* for the two frequently named muscles whose relative proportions in most mammals are so misrepresented by the adjectives *major* and *minor*.

II. 1880–83. While preparing a paper on the brain of the cat, and (with S. H. Gage) a volume of directions for laboratory work, I adopted from Barclay the unambiguous toponyms *dorsal*, *dorsad*, etc.; replaced his *mesion* by *meson*, the direct paronym of *μέσον*; added *ectal*, *ental*, etc.; and simplified some organonyms, especially muscular and neural, in the following ways: (*a*) Dropping unessential adjectives (*opticus* from *thalamus* and *chiasma*); eponymic (§ 33) qualifiers (*Varolii*, *Reilii*, *Rolando*); and generic nouns (*corpus*, *mater*, and *membrana*) from adjectives that were sufficiently distinctive and could be used as substantives (*callosum*, *dura*, *mucosa*); (*b*) substituting prepositions for adjectives (*e.g.*, *postcommissura* for *commissura posterior*); (*c*) replacing certain polyonyms by mononyms more or less nearly akin thereto (*e.g.*, *lamina terminalis* by *terma*);

[1] On several previous occasions I have shown that analogy with words like *angel* and *angelic* (from ἄγγελος) calls for *myel* and *myelic* as the English nominative and adjective of *myelon; myelonal* is clumsy, and analogy would involve the replacement of *encephalic* by *encephalonal*.

[2] The foregoing first appeared half a century ago; the mononym *myelon* was employed consistently by Owen, and on at least one occasion by his rival Huxley. These facts should secure for it the consideration due to high authority and moderate antiquity, and forestall any hasty proposition to employ it in a different sense.

and (*d*) abandoning the anthropotomic misnomers of the encephalic cavities in favor of mononyms coördinated with the commonly accepted titles of the encephalic segments (*e.g.*, *Aquaeductus Sylvii* and *Iter a tertio ad quartum ventriculum* for *mesocoelia*).[1]

Notwithstanding their defects, these efforts to improve anatomic language elicited favorable comment, helpful criticism, and more or less actual adoption from Oliver Wendell Holmes ('81), Joseph Leidy ('85, '89),[2] Henry F. Osborn ('83, '84), E. C. Spitzka ('81), and R. Ramsay Wright ('85).

III. 1884–88. Although now satisfied as to the correctness of the general system and as to the excellence of most of the individual terms, I began to realize more fully the magnitude and difficulty of the task and the necessity for counsel and coöperation. In the summer of 1884, at my suggestion, committees were appointed by the American Neurological Association and the American Association for the Advancement of Science. The constitution of these committees (p. 126) insured that no hasty action would be taken, and warranted the hope that any conclusions reached by them would be considered seriously here and abroad. Personal conferences were held when practicable, but most of the work of comparing views and preparing preliminary reports was done by correspondence.

As collaborator on a medical dictionary (Foster, '88–'94), I undertook to obtain a list of names already applied to parts of the central nervous system. In 1888 the total was 10,500, distributed as follows in round numbers: Latin, 3100; English, 1800; French, 1800; Italian and Spanish, 900; German, 2900. Assuming the number of parts or features to be 500–600, there were evidently many superfluous neuronyms, especially in Latin

[1] Nothing in my terminologic experience has been more gratifying and encouraging than the approximate coincidence of a similar proposition by T. Jeffery Parker ('82, '84).

[2] While engaged upon the new edition of his *Anatomy*, Professor Leidy wrote me under date of Jan. 20, 1885: "I wish to aid in reforming the nomenclature of anatomy, and in doing so propose to anglicize the names to some extent [p. 114]. Will you please look over this list of muscles and tell me whether I can do better with any of the names." Ten days later he submitted a list of the neural terms. Many of my suggestions were adopted.

and German. The excess in these two languages might be accounted for in part by the international character of the former and by the large number of publications in the latter.

But a careful scrutiny disclosed two other causes: (1) Many of the Latin names, especially the older, comprised so many words as to constitute descriptive phrases, and to furnish opportunity for conscious or unconscious abridgment and permutation (p. 113); each resultant combination had to be regarded as a name. In W. & G. ('89), § 56, are enumerated no less than twenty-three distinct Latin names for the fibrous bundle connecting the cerebellum with the oblongata; they average nearly 2.7 words each.[1]

(2) Of the German names but a small proportion (58, or two per cent of the total) had any obvious resemblance to equivalent Latin terms (*Fissur* to *fissura*, *Commissur* to *commissura*, *Centralcanal* to *canalis centralis*); the vast majority were vernacular translations (*e.g.*, *Brücke*, *Schenkel*, *Seepferdefuss*, *Schhügelpolster*).[2] Different writers made different translations, and considerable variation occurred in different parts of the same publication (p. 112). Hence there arose a multitude of terms, acceptable and intelligible only to readers of the same nationality, and bearing no relation to the original or international Latin terms. In a greater or less degree the same might be said of the other modern languages.

It will be seen that two opposing influences were operating. Each anatomist preferred to employ terms belonging to his own language; at the same time he preferred that other anatomists should employ Latin terms with which he was already familiar, or which were intelligible without an intimate acquaintance with other modern languages than his own.

With a view to reconciling these two opposing tendencies I formulated ('85) the distinction between heteronyms and paronyms, and proposed that, with few exceptions, heteronyms should be discarded in favor of paronyms. "Since each paronym suggests the original Latin name, the latter forms a bond

[1] All these might be replaced by the single word *postpedunculus*.

[2] Without imputing even so worthy a motive as national self-satisfaction, the effect was as if certain neurologists had yielded to a desire to confer upon the printed page an obtrusively German aspect.

of intelligence between writers and readers of different nationalities."

The international advantages of paronyms over heteronyms have been distinctly recognized, and the principle indorsed, by the American branch of the International Committee of Biological Nomenclature and by the American Association for the Advancement of Science (Proceedings, 1892, 233).

That mononyms are more readily and uniformly paronymized than polyonyms, and dionyms than other polyonyms, has been already mentioned (p. 116) and is, indeed, self-evident.

IV. 1889–94. But the recognition of the nature and causes of neuronymic hypertrophy and deformity, and even the formulation of general principles of relief, still left unaccomplished the necessary operations of excision and correction. My inability to decide in season which should be regarded as *the* names, and which as merely synonyms, was one of the reasons for not accepting the invitation of Dr. Foster to frame the definitions in the dictionary above mentioned. Partial lists had been prepared in connection with the *Anatomical Technology* ('82) and the *Cartwright Lectures* ('84). The latter list contained 115 names, exclusive of the fissures, and gyres, and blood-vessels. In connection with a paper, entitled "Owen's Nomenclature of the Brain" ('90), there was presented to the Association of American Anatomists a "Macroscopic Vocabulary" of about 200 names, with synonyms and references. The vessels, fissures, and gyres were estimated at 140, and lists of them were published at various periods ('85, '86).

This made a total of about 340 parts or features of the central nervous system, the designations of which I had selected or framed from among the vast accumulation of available terms. These names had already been found serviceable in the research and instruction carried on under my direction; they were embodied in the articles on the gross anatomy of the brain;[1] and questions involved in their adoption were discussed by S. H. Gage and myself in "Anatomical Terminology" ('89).

[1] Brain, gross or macroscopic anatomy, Buck's Reference Handbook of the Medical Sciences, VIII, pp. 58, 104 figs., 1889. Brain, malformations of, which are morphologically instructive, *same*, pp. 6, 10 figs. Brain, removal, preservation and dissection of, *same*, pp. 7, 5 figs.

V. 1895–96. Among the requirements of technical terms enumerated in 1871 was "Independence of context for signification." The rigid application of this would exclude all homonyms and would require every term to be absolutely explicit. It was perhaps not unnatural for a comparative beginner in the subject to make such a rule, and, having made it, to adhere to it somewhat persistently, as in the following cases.

Of the three current appellations, *conarium*, *epiphysis*, and *corpus pineale*, the last was rejected unhesitatingly as a polyonym, and the second as applying equally (without the qualifier *cerebri*) to the separable end of a growing bone; as recently acknowledged ('96), I long resisted the precept and example of H. F. Osborn and E. C. Spitzka in favor of *epiphysis* as correlative with *hypophysis*, and failed to recognize the full force of Dall's remark, "The human mind wearies of too many names, and much more readily assimilates a new meaning for an old one."

Likewise, although favoring the general plan of rendering the Latin *ae* and *oe* by *e* in anglicized (paronymized) words,[1] I retained the diphthong in *coelia* and its compounds (from κοιλία, a cavity) for the sake of distinguishing them from the derivatives of κήλη, a tumor. I now frankly acknowledge the non-necessity of the diphthong even for the discrimination of *encephalocele*, the normal cavity of the brain, from the same word signifying an abnormal protrusion of the organ.

In August, 1884, I proposed to replace the common polyonym, *axis cerebro-spinalis*, and even Owen's *myelencephalon*, by the brief mononym, *neuron*, warranted by *neuralis*, *neurentericus*, etc., and correlated with *enteron* (*canalis alimentaria*) and *axon* (*axis somatica*). The term was used by Minot ('92), Stowell ('85), Waters ('91), and others. Its abandonment by me in favor of *neuraxis* ('89) was due to two later observations: (*a*) the prior use of *neuraxis*[2] in the same sense; (*b*) the prior application of

[1] In this country no medical writer has more persistently and vigorously urged this simplification than the former editor of the *Medical News*, Gould, George M. ('94, '96).

[2] In the Dictionnaire de Médecin of Robin and Littré occurs *nèvraxe*, the Galloparonym of a potential antecedent, *neuraxis;* but neither the propounder nor the first adopter is named.

neuron to a part of an invertebrate eye. I have since been led to believe that I was unduly influenced by these considerations. Unfortunately, the matter is now complicated by (*a*) the application of *neuron* to the entire nerve-cell, including its processes, and (*b*) the designation of the "axis-cylinder process" by *neuraxon*, easily confounded with neuraxis.[1] I have already declared ('93, '95) my lack of personal feeling in the matter, but the more I think of it the greater appear to me the advantages of *neuron*. In view of the practical efficiency of "contextual explicitness," its "invertebrate" use may be ignored, and where there could be any doubt as to whether *neuron* referred to the entire nervous axis or only to one of its histologic constituents *macroneuron* and *microneuron* might be employed. Cases not strictly analogous and yet worthy of note in this connection are the general use of *body* and *belly* for parts of a muscle, and of *tarsus* and *cilium* in both macroscopic and microscopic senses. Whatever may be the outcome, I shall always regret the confusion arising from what I now regard as a manifestation of excessive conscientiousness.

Terms Withdrawn. — Through ignorance, misapprehension, timidity, or over-confidence, I have at various times proposed or employed needless or objectionable terms. Their formal withdrawal is here made in accordance with a conviction which was expressed ('91) five years ago: "Since every one makes mistakes, the interests of all concerned would be subserved by the adoption of the custom of each correcting his own, either as soon as discovered or periodically ; a sort of scientific confession of sins. The natural corollary to this would be that each well-disposed discoverer of another's fault would inform him privately, so that he might make prompt correction. This plan I have followed in several cases, and have reason to believe it has served to avoid personal irritation and the needless repetition of criticism."

The following terms are hereby withdrawn: *Hypocampa* (for *hippocampus* [*major*]), *Torus* (for *tuber* [*cinereum*]), *Lenum* (for *torcular* [*Herophili*]), *Cerebrocortex* (for *cortex cerebri* or *cerebral*

[1] For some history and discussion of these and kindred terms see the papers of Fish ('94) and Baker ('95).

cortex), *Cerebellocortex* (for *cortex cerebelli* or *cerebellar cortex*), *Commissure habenarum* (for *supracommissura*), *Mediventricle* (for "third ventricle"), *Lateventricle* (for "lateral ventricle"), *Procele* (for paracele), *Coele* and its compounds (for cele and its compounds).

If the foregoing list of my verbifactive sins appears damagingly large, let the critics scan their own records with equal closeness; I have at least been consistent within the limits of a single publication.

Acknowledgments. — I have had more or less frequent conference or correspondence with nearly all the members of the four committees named elsewhere and with other scientific or literary authorities. Only by investigators, teachers, and practitioners equally eminent, preoccupied, and familiar with current terminology, can it be wholly realized what it meant for these men to give prompt and full attention to queries and propositions that threatened to disturb the verbal basis of their intercommunications. Reviewing the experience, I am amazed at the uniform readiness and kindliness of the responses,[1] and can truly say that, even when not wholly or directly encouraging, they were always fruitful. To four men are due particular acknowledgments.

As student (1873–77), as assistant (1875–80), as colleague (since 1880), and as collaborator (*Anatomical Technology*, 1880–92; *Anatomical Terminology*, 1888–89), Simon H. Gage has been constantly and preëminently helpful.

Edward C. Spitzka, one of the most learned, progressive, and productive American neuro-anatomists, generously entertained the new terms ('81), adopted some, and for others proposed improvements; nay, this undaunted upholder of an unpopular opinion in a period of intense political excitement[2] went so far as to say that some of my suggestions had been long in his own mind, but that he had "lacked the courage to

[1] Their nature made it the easier to meet with equanimity the few attempts to check terminologic progress by ridicule. For the response to one of these, see my paper, "The Paroccipital Fissure. Letter to the Editor." *N. Y. Med. Record*, Oct. 2, 1886, pp. 389, 390.

[2] As an expert at the trial of Guiteau he held the mental constitution of the assassin to be abnormal; see *Alienist and Neurologist*, 1883, April, *et seq.*

bring them before his colleagues." Dr. Spitzka's cordial interest has never abated, and I only lament that more practical duties leave him less time now than formerly for research in the anatomy of the brain.

I have already expressed my appreciation of the erudition and kindness of my colleague in comparative philology, Benjamin I. Wheeler. Aside from information imparted at personal interviews, the etymologic and linguistic points upon which he has enlightened me cover nearly one hundred of the "correspondence slips."

To quote his own words, "The last thing an old teacher wants is a new set of terms for a familiar set of objects." Yet this did not prevent Oliver Wendell Holmes, then for the third of a century professor of anatomy in the Harvard Medical School, from writing, May 3, 1881, a letter containing the following passages: —

"I have read carefully your paper on nomenclature. I entirely approve it as an attempt. I am struck with the reasonableness of the system and the fitness of many of the special terms. The plan is an excellent one; it is a new garment which will fit Science well, if that capricious and fantastic and old-fashioned dressing lady can only be induced to try it on."

This letter was a source of comfort to me, and doubtless led many to consider seriously suggestions that might otherwise have been ignored or repelled.

On the 5th of June, 1896, at a regular meeting in Philadelphia, the American Neurological Association adopted unanimously the "Report of the Committee on Neuronymy."[1] The recommendations were as follows: —

[1] The committee was appointed by the president of the Association, upon the suggestion of the writer, at the regular meeting in New York City, June 20, 1884. One of the most interested of the original members, Dr. W. R. Birdsall, has since died. It now comprises Henry H. Donaldson, Ph.D., professor of neurology, Chicago University; Landon Carter Gray, M.D., professor of nervous and mental diseases, New York Polyclinic; Charles K. Mills, M.D., professor of diseases of the mind and nervous system in the Philadelphia Polyclinic; Edward C. Seguin, M.D., professor of diseases of the mind and nervous system in the Medical Department of Columbia University; Edward C. Spitzka, M.D., formerly professor of the anatomy and physiology of the nervous system in the Post-graduate Medical School of New York City; and B. G. Wilder, chairman.

(1) That the adjectives DORSAL and VENTRAL be employed in place of *posterior* and *anterior* as commonly used in human anatomy, and in place of *upper* and *lower* as sometimes used in comparative anatomy.

(2) That the cornua of the spinal cord and the spinal nerve-roots be designated as DORSAL and VENTRAL rather than as *posterior* and *anterior*.

(3) That the costiferous vertebrae be called THORACIC rather than *dorsal*.

(4) That, other things being equal, MONONYMS (single-word terms) be preferred to *polyonyms* (terms consisting of two or more words).

(5) That the *hippocampus minor* be called CALCAR; the *hippocampus major*, HIPPOCAMPUS; the *pons Varolii*, PONS; the *insula Reilii*, INSULA; *pia mater* and *dura mater*, respectively, PIA and DURA.

(6) That the following be employed rather than their various synonyms: HYPOPHYSIS, EPIPHYSIS (for *conarium* and *corpus pineale*), CHIASMA, OBLONGATA, LEMNISCUS, MONTICULUS, TEGMENTUM, PULVINAR, FALX, TENTORIUM, THALAMUS, CALLOSUM, STRIATUM, DENTATUM, MESENCEPHALON, PALLIUM, OLIVA, CLAVA, OPERCULUM, FISSURA CENTRALIS (for *f. Rolando*, etc.), F. CALCARINA, F. COLLATERALIS, F. HIPPOCAMPI, CUNEUS, PRAECUNEUS, CLAUSTRUM, FORNIX, INFUNDIBULUM, VERMIS.

Sections 1, 2, 3, and 5 constituted the "Preliminary Report of the Committee on Anatomical Nomenclature" of the Association of American Anatomists, which was adopted unanimously by that body Dec. 27, 1889.[1]

Section 4 is substantially identical with the second paragraph of the "Second Preliminary Report" of the same

[1] The members of the committee at that time were Joseph Leidy, M.D., LL.D., professor of anatomy in the University of Pennsylvania, president; Harrison Allen, M.D., formerly professor of physiology in the University of Pennsylvania; Frank Baker, M.D., professor of anatomy in the Medical Department of Georgetown University; Thomas B. Stowell, Ph.D., principal of the Potsdam (N.Y.) Normal School; and B. G. Wilder, secretary. To the committee, at the meeting, was added Thomas Dwight, M.D., professor of anatomy in the Harvard Medical School. The report was published in the History and Records of the Association for 1888, 1889, 1890, p. 5.

committee,[1] *viz.*, "Your committee recommend to anatomists that, other things being equal, terms consisting of a single word each be employed rather than terms consisting of two or more words." *Proceedings* for 1895, p. 4.

Section 4 is also substantially represented in the "Third Preliminary Report of the Committee on Anatomical Nomenclature with Special Reference to the Brain,"[2] which was adopted unanimously by the American Association for the Advancement of Science, Sept. 2, 1889: "They agree upon one point, *viz.*, the advantages, other things being equal, of mononyms (single-word terms) over polyonyms (terms consisting of two or more words)." The report was published in the *Proceedings* for 1889, page 26.

Sections 1, 2, 3, 5 occur *verbatim* in the fourth report of the same committee, which was adopted unanimously by the Association Aug. 25, 1890, and printed in the *Proceedings*, page 20.

The first five sections of the report of the Neurological Committee are embodied *verbatim* in the "Preliminary Contribution of the American Branch of the International Committee on Biological Nomenclature of the American Association for the Advancement of Science,"[3] which was adopted unanimously by that body Aug. 23, 1892, and published in its *Proceedings*, page 231.[4]

The report just mentioned is so clear, comprehensive, and concise that its main features are here summarized:

[1] Upon the death of Dr. Leidy, Dr. Allen succeeded to the chairmanship of the committee. The place of Dr. Stowell, resigned on account of pressing administrative duties, was filled by the appointment of F. H. Gerrish, M.D., professor of anatomy in the Medical School of Maine.

[2] The committee comprised, besides H. Allen, F. Baker, T. B. Stowell, and B. G. Wilder, chairman, Henry F. Osborn, Sc.D., professor of biology in Columbia University.

[3] The members are George L. Goodale, Ph.D., professor of natural history in Harvard University, chairman; John M. Coulter, LL.D., president of the State University of Indiana; Theodore Gill, Ph.D., Smithsonian Institution; Charles Sedgwick Minot, Ph.D., professor of embryology in Harvard University; Simon H. Gage, B.S., professor of histology and embryology in Cornell University, secretary.

[4] Reprints were distributed to biologists of all nationalities, and may be obtained from the secretary.

(*a*) "Terms relating to position and direction [toponyms] should be intrinsic rather than extrinsic; that is, should refer to the organism itself rather than to the external world."

(*b*) "So far as possible, terms should be single, designatory words [mononyms] rather than descriptive phrases."

(*c*) Terms derived from the names of persons [eponyms] should be avoided.

(*d*) "Each term should have a Latin [international] form."

(*e*) "Each term should have also a [national] form in accordance with the genius of each modern language, *e.g.*, a paronym of the original Latin form."

(*f*) The report gives due recognition of the labors of other committees and of individuals.

Returning to the report adopted by the American Neurological Association, its recommendations may be indicated conveniently in Table I.

It should be borne in mind that only the Latin names in the first column have the sanction of the various associations that have adopted them. The derivatives and the comments thereon do not constitute parts of the reports. Indeed, as will be seen, there is room for considerable latitude of opinion and usage; my own views may be imperfect and even inconsistent, but I think the analogies adduced are sound.

English Plurals. — The parts of the brain are so seldom named in the plural that a separate column is not given therefor. Analogy with *crises*, *strata*, *fungi*, *algae*, and *phenomena* would justify the employment of the regular Latin plural in certain cases, *e.g.*, *thalami*, *epiphyses*, *hippocampi*, *cornua*, *striata*, and *vertebrae*. On the other hand, *areas*, *vistas*, *hernias*, *emporiums*, *lenses*, *geniuses*, *pianos*, *indexes*, *pericarps*, *angles*, *atlases*, *diplomas*, and *similes* are precedents for *calcars*, *chiasmas* (or chiasms), *falxes*, *hippocamps*, *insulas*, *mesencephals*, *ponses*, *vermises*. *Bonuses* would even justify *thalamuses*, but the length of the latter is objectionable.

Close Resemblance of the Angloparonyms to the Latin Originals. — This is so obvious as to hardly require mention. With more than half the two forms are identical in spelling, so that the Latinity of the originals can only be indicated to the eye

TABLE I.

Derivatives of the terms adopted by the American Neurological Association.

	SUBSTANTIVES.		ADJECTIVES.	
	LATIN	ENGLISH	LATIN	ENGLISH
1	Calcar	Calcar	Calcarinus	Calcarine
2	Callosum	Callosum	Callosalis	Callosal
3	Chiasma	Chiasma or chiasm	Chiasmaticus	Chiasmatic
4	Claustrum	Claustrum	Claustralis	Claustral
5	Clava	Clava	Clavalis	Claval
6	Cornu dorsale	Dorsal cornu		
7	Cornu ventrale	Ventral cornu		
8	Cuneus	Cuneus	Cunealis	Cuneal
9	Dentatum	Dentatum	Dentatalis	Dentatal
10	Dura	Dura	Duralis	Dural
11	Epiphysis	Epiphysis	Epiphysialis	Epiphysial
12	Falx	Falx	Falcialis	Falcial
13	F. calcarina	Calcarine fissure		
14	F. centralis	Central fissure		
15	F. collateralis	Collateral fissure		
16	F. hippocampi	Hippocampal fissure		
17	Fornix	Fornix	Fornicalis	Fornical
18	Hippocampus	Hippocamp or hippocampus	Hippocampi (gen.) or hippocampalis	Hippocampal
19	Hypophysis	Hypophysis	Hypophysialis	Hypophysial
20	Infundibulum	Infundibulum	Infundibularis	Infundibular
21	Insula	Insula	Insularis	Insular
22	Lemniscus	Lemniscus	Lemniscalis	Lemniscal
23	Mesencephalon	Mesencephal or mesencephalon	Mesencephalicus	Mesencephalic
24	Monticulus	Monticulus	Monticularis	Monticular
25	Oblongata	Oblongata	Oblongatalis	Oblongatal
26	Oliva	Oliva or olive	Olivaris	Olivary
27	Operculum	Operculum or opercle	Opercularis	Opercular
28	Pallium	Pallium	Pallialis	Pallial
29	Pia	Pia	Pialis	Pial
30	Pons	Pons	Pontilis	Pontile
31	Praecuneus	Precuneus	Praecunealis	Precuneal
32	Pulvinar	Pulvinar	Pulvinaris	Pulvinar
33	Striatum	Striatum	Striatalis	Striatal
34	Tegmentum	Tegmentum or tegment	Tegmentalis	Tegmental
35	Tentorium	Tentorium	Tentorialis	Tentorial
36	Thalamus	Thalamus	Thalamicus	Thalamic
37	Radix dorsalis	Dorsal root		
38	Radix ventralis	Ventral root		
39	Vermis	Vermis	Vermianus	Vermian
40	Vertebra thoracalis	Thoracic vertebra		

by italics and to the ear by the pronunciation now commonly adopted for Latin words.[1]

Hippocamp. — For this, as the Angloparonym of hippocampus, there are many precedents, notably the following: *antepenult*, *digit*, *impediment*, *diagram*, *telegram* (which was strenuously objected to when first introduced), *epicarp*, and *pericarp*.

Infundibulum. — If the part so designated were frequently mentioned it is probable that either a shorter word would be found or the present name be paronymized as *infundibule*, after the analogy of *reticule*, *diverticle*, etc. The same may be said of *monticulus* and *monticule*.

Mesencephalon. — By itself and used occasionally, the Latin form is certainly euphonious and unobjectionable; but in any discussion of the segmental constitution of the brain, whether written or spoken, the frequent recurrence of the obtrusively Latin termination is pedantic and burdensome. Its omission is warranted by words like *angel*.

Operculum and *Opercle.* — The Latin tetrasyllable is not commonly oppressive, but the compounds *preoperculum*, etc., might well become so. The case is comparable with that of *ultima;* with it, and even with *penultima*, the last two syllables are endured; but when two more syllables are added at one end, then two are dropped from the other, leaving *antepenult* of only moderate length. *Preopercle*, *subopercle*, and *postopercle* are already applied to analogous parts of the fish's head, but the chance of misapprehension is very slight.

Praecuneus. — Here the difference between the Latin antecedent and the Angloparonym consists in the replacement of the *ae* by *e*, as in *preposition*, *pretext*, *preface*, etc.

Tentorium. — By analogy with *ovary*, *aviary*, *granary*, *laboratory*, etc., the Angloparonym would be *tentory*, and this word has been used to designate the awning of a tent. But *tentorium* is unobjectionable and likely to be retained as an unchanged paronym.

[1] The Angloparonyms of Latin words, even when orthographically unmodified, are English by adoption, and are to be so pronounced; to pronounce *claustrum*, *clowstroom* in an English sentence would be as affected as to say *mamorarndoom*. As an English word *oblongata* has the first *a* as in *mate*.

Pontilis. — Unwarrantable forms of the English adjective from *pons* occur so frequently that there is here reproduced a paragraph from my recent note on the subject ('96a). "In the subtitle of the letter above mentioned, the case is referred to as one of '*pontine* hemorrhage.' This form of the adjective is not uncommon in medical literature, and *pontic* and *pontal* have found their way into the dictionaries. Now, as may be seen from any Latin lexicon, *pontal* has no justification whatever. *Ponticus*, the Latin antecedent of *pontic*, is derived from *pontus*, the sea. *Pontinus*, the antecedent of *pontine*, was originally *Pomptinus*, and refers to a district of Italy. As already pointed out by me (article "Anatomical Terminology," *Buck's Reference Handbook of the Medical Sciences*, VIII, 524, § 50), the only legitimate Latin adjective from *pons* is *pontilis*, and its Angloparonym is *pontile*. The use of any other form tends to cause confusion and to bring discredit upon medical scholarship."

In Table II on the following pages are given in parallel columns (1) the forty terms adopted by the American Neurological Association; (2) the corresponding terms adopted by the Anatomische Gesellschaft; (3) some of the Latin synonyms.

Probably few will question the inferiority of the discarded synonyms in the third column; hence I have here considered mainly the relative merits of the two other sets.

The extent of agreement is impressive and encouraging. With the following twenty-four terms there is absolute consensus between the American and the German committees: Claustrum, Clava, Cuneus, Fissura calcarina, F. collateralis, F. hippocampi, Fornix, Hippocampus, Hypophysis, Infundibulum, Insula, Lemniscus, Mesencephalon, Monticulus, Oliva, Operculum,[1] Pallium, Pons, Praecuneus, Pulvinar, Tegmentum, Thalamus, Vermis, Vertebra thoracalis.

[1] The case of this term is peculiar. The German committee particularize three parts, *frontal*, *parietal*, and *temporal* of a general operculum. The Neurological Association regards the parietal portion as *the* operculum, the frontal and temporal being so specified. (By the present writer these are designated as *praeoperculum* and *postoperculum*, and the *orbital* portion as *suboperculum*.) It will be seen, therefore, that, while the word *operculum* is identical with both committees, its significance is general with the German and special with the American.

Table II.

Comparison of the terms adopted by the American Neurological Association (first column) with those of the German committee (second column) and with certain synonyms (third column).

1	Calcar	Calcar avis	Hippocampus minor; Eminentia digitalis; Unguis
2	Callosum	Corpus callosum	Corpus callosum; Trabs cerebri
3	Chiasma	Chiasma opticum	Chiasma nervorum opticorum; Commissura optica
4	Claustrum	Claustrum	Claustrum
5	Clava	Clava	Processus clavatus
6	Cornu dorsale	Columna posterior	Cornu posterius
7	Cornu ventrale	Columna anterior	Cornu anterius
8	Cuneus	Cuneus	Lobulus occipitalis internus; Lobulus cuneatus
9	Dentatum	Nucleus dentatus	Corpus dentatum cerebelli
10	Dura	Dura mater	Dura mater
11	Epiphysis	Corpus pineale	Conarium; Glandula pinealis; Epiphysis cerebri
12	Falx	Falx cerebri	Falx major; Processus falciformis
13	Fissura calcarina	Fissura calcarina	Fissura occipitalis horizontalis
14	Fissura centralis	Sulcus centralis	Fissura Rolandica; Sulcus postero-parietalis
15	Fissura collateralis	Fissura collateralis	Sulcus occipito-temporalis; S. temporo-occipitalis
16	Fissura hippocampi	Fissura hippocampi	Fissura hippocampi
17	Fornix	Fornix	Fornix tricuspidalis
18	Hippocampus	Hippocampus	Hippocampus major; Cornu Ammonis
19	Hypophysis	Hypophysis	Glandula pituitaria; Hypophysis cerebri
20	Infundibulum	Infundibulum	Pedunculus hypophyseos
21	Insula	Insula	Insula Reillii; Lobus centralis; Median lobe
22	Lemniscus	Lemniscus	Laqueus

23	MESENCEPHALON	Mesencephalon	Mesencephalon
24	MONTICULUS	Monticulus	Monticulus
25	OBLONGATA	Medulla oblongata	Bulbus rhachidicus
26	OLIVA	Oliva	Corpus olivare ; Nucleus olivaris
27	OPERCULUM	Operculum (pars parietalis)	Operculum parietale
28	PALLIUM	Pallium	Mantellum
29	PIA	Pia mater	Pia mater
30	PONS	Pons [Varolii]	Pons Varolii ; Protuberantia annularis
31	PRAECUNEUS	Praecuneus	Lobus quadrilaterus
32	PULVINAR	Pulvinar	Tuberculum [thalami] posterius
33	STRIATUM	Corpus striatum	Ganglion cerebri anterius
34	TEGMENTUM	Tegmentum	Tegmentum caudicis
35	TENTORIUM	Tentorium cerebelli	Tentorium
36	THALAMUS	Thalamus	Thalamus opticus ; T. nervi optici ; Ganglion cerebri posterius
37	RADIX DORSALIS	Radix posterior	Radix posterior
38	RADIX VENTRALIS	Radix anterior	Radix anterior
39	VERMIS	Vermis	Vermis bombycinus ; Processus vermiformis
40	VERTEBRA THORACALIS	Vertebra thoracalis	Vertebra dorsalis

With the following ten terms the differences lie merely in the retention by the Germans of certain words which the Americans regard as superfluous. In the list these words are italicized: Calcar *avis*, *Corpus* callosum, Chiasma *opticum*, *Nucleus* dentatus, Dura *mater*, Falx *cerebri*, *Medulla* oblongata, Pia *mater*, *Corpus* striatum, Tentorium *cerebelli*. With the remaining six terms the differences are more or less radical.

Calcar vs. *calcar avis*. — Thirty years ago, in connection with the controversy as to the cerebral peculiarities of man, the term *hippocampus minor* became familiar even to general readers. Nevertheless, probably influenced in some degree by Huxley's proposition to replace Owen's *posthippocampal* and Henle's *occipitalis horizontalis* by *calcarina*,[1] anatomists have been more and more generally employing *calcar avis*, and this is adopted by the German committee in preference also to *unguis* and *eminentia digitalis*. The advantages of correlated names for collocated parts are many and great, as illustrated by *hippocampus* [*major*] and *fissura hippocampi*; by *eminentia collateralis* and *fissura collateralis*. In the present case these advantages would have been gained equally had Huxley adopted Owen's *posthippocampal* for the fissure and proposed *posthippocampus* for the ental ridge corresponding thereto. Indeed, this would have been in accordance with the general principle of locative names, and learners would have been spared thereby some effort of memory. In this, however, as in so many other instances, it is now idle to speculate upon the consequences of harmonious coöperation between the two leaders of English anatomy at that period. Assuming that *calcar avis* has general and decided preference over the other names enumerated, there need be stated here only the grounds upon which *calcar* has been unanimously adopted by four American committees and by the three associations which they represent.

Briefly, the adoption of *calcar* is a logical corollary of the recommendation which is common to the reports of all four American committees, *viz.*, "Other things being equal, it is

[1] Pye-Smith wrote as follows nearly twenty years ago ('**77**): "Of all the synonyms of *hippocampus minor*, *calcar avis* is the most distinctive and brings it at once into relation with the calcarine fissure."

recommended that mononyms be preferred to polyonyms." *Calcar avis* is a polyonym; *calcar* is a mononym.

If it be said that *unguis* is also a mononym, the answer is that in this case "other things" would not be equal, because (1) no general preference has ever been shown for it or for any term of which it is a constituent; (2) there would be lost the advantage of the correlation now existing between the ental ridge and the fissure collocated therewith.

Two objections might be offered to the omission of the qualifying genitive, *avis*.

(1) The original sense of the Latin *calcar* was *spur*, and its application to the sharp projection on the leg of the cock was metaphoric. This can hardly be entertained as a serious objection; indeed, although the modern spur has a toothed wheel or rowel, the primitive instrument was little more than a spike; hence the qualifying genitive is needless.

(2) *Calcar* has also been applied occasionally to two other parts, *viz.*, the calcaneum (os calcis) and the styloid process of the temporal bone. But (*a*) neither of these uses is sanctioned by the German committee, and (*b*) even if they were, the context would infallibly avert misapprehension (p. 113); indeed, the German committee apply *clivus* without qualification to features of two adjacent cranial bones, the occipital and sphenoidal.

Finally, the sufficiency of the mononymic substantive, *calcar*, is practically conceded by all who employ the mononymic adjective, *calcarinus*, in any of its Latin inflections, or in any of its national paronymic forms. The simplest requirements of logic present the following dilemma: If *calcarinus* is sufficiently distinctive, so is *calcar*, from which it is derived. But if *calcar avis* is essential, then the adjective should be *calcari-avianus* or some such compound. See also under *dura*. There seems to have been little, if any, hesitation on the part of the German committee in adopting *fissura calcarina* (His, '96, 170), and no reason for the maintenance of *calcar avis* has yet come under my notice.

CHIASMA vs. *chiasma opticum*. — Meynert's *chiasma nervi acustici* is not retained by the German committee, and, even if

it were, there is no likelihood of confusion with it or with Camper's *chiasma tendinum*. *The* chiasma is and always will be that of the optic nerves. The use of any qualifier suggests undesirable variations, like *chiasma nervorum opticorum* and *commissura optica*. Furthermore, the sufficiency of the unincumbered mononym is practically conceded by the German committee in designating one of the subarachnoid spaces as *cisterna chiasmatis;* see also His ('95), 171, line 8.[1]

Thalamus. — This term may naturally be mentioned here. In the German list the adjective *opticus* is omitted, and His makes the following remark ('95, 7, lines 1–3): "Wir stimmen unsererseits völlig bei, wenn das Wort Thalamus kurzweg an die Stelle von Thalamus opticus gesetzt wird." But it is worthy of note that *thalamus* is strictly an idionym, and that the only valid excuse for the addition of the adjective is a desire to aid the student's memory by the association with the optic nerve. As a matter of fact, no case of real advantage is known to me, and the frequent repetition of the adjective may easily become a burden, as pointed out by me in 1888.

Callosum vs. *corpus callosum.*—*Corpus callosum* is the most familiar type of a large group of anatomic names. In 1889, including unusual synonyms, I recorded one hundred neural polyonyms of which *corpus* constituted the initial word. Ten such remain upon the German list (*viz.*, *corpus restiforme*, *cp. trapezoideum*, *cp. medullare*, *cp. quadrigeminum*, *cp. mamillare*, *cp. geniculatum mediale*, *cp. gnc. laterale*, *cp. pineale*, *cp. callosum*, *cp. striatum*), and their genitives are correspondingly in evidence.

It must be admitted that *corpus callosum* is rather attractively sonorous. It is easily pronounced, and even, like *quadrupedante*, "runs trippingly from the tongue."[2] But that is no reason for the retention of a word which is not merely needless, but really burdensome by reason of the frequency with which certain parts are mentioned. In one short paper (*Brain*, October, 1885, 377–379) *corpus callosum* occurs twenty times,

[1] The word *chiasma* is discussed at some length by Hyrtl ('80).

[2] A similar concession has been made (*Science*, June 22, 1888, editorial) to the claims of proper names like *Johnny McWhorter*, which are euphonious and easily remembered.

an average of once in five lines; *corpus* occupies 2.5 lines, one-fortieth of the entire paper.

The elimination of *corpus* from all neural names constituted one of the fundamental propositions of my first communication upon the general subject ('80), and since that time it has been consistently practised and persistently preached.

By the use of the genitive case, *corporis callosi*, the German committee have designated the various divisions of the callosum (splenium, genu, truncus, and rostrum); also the sulcus along its dorsal margin. They have thus avoided the use of the secondary adjective *callosalis*. But in expressly rejecting *pedunculus corporis callosi* in favor of *gyrus subcallosus* (His, '95, 170–172), they practically concede the superfluity of the *corpus*.

Unless we are prepared to abandon all adjective substantives, there seems to be no reason for the further retention of *corpus* in any of the terms enumerated. *Corpus fornicis* of the German list is not open to the objection that naturally arises against *corpus corporis callosi*, but *truncus corpus callosi* is a good precedent for *truncus fornicis*, if the distinction be necessary.

Dura vs. *dura mater*. — This constitutes a type and test case for a considerable group of anatomic terms from which, for fifteen years, I have dropped the nouns (here italicized), *viz.*, pia *mater*, *substantia* alba, *substantia* cinerea, *membrana* (or *tunica*) serosa, *mb.* (or *tn.*) mucosa, *mb.* (or *tn.*) submucosa, *mb.* (or *tn.*) arachnoidea, *medulla* oblongata. They differ from the group of "corpus" polyonyms, in that the elimination of the substantive leaves a feminine instead of a neuter adjective to be used substantively and as a base for the formation of secondary adjectives, *dural*, *mucosal*, *cinereal*, *arachnoidal*, etc.

Curiously enough, the first precedent for this known to me dates back a hundred and fifty years. In the *Medical Dictionary* of James (1743), in the article "Cerebrum" occurs the following sentence: "The superficial vessels of the cerebrum are lodged between the two laminae of the pia."

The employment of the mononymic feminine adjectives as substantives and of the secondary adjectives derived therefrom

has now become so general[1] that the matter would hardly need discussion but for the reactionary attitude of the German committee. Yet this attitude is really not maintained consistently. *Cornea* is a feminine adjective; so is *sclera*. In *arachnoidea encephali* the feminine adjective is used as a noun. *Muscularis mucosae* and *tela submucosa* are warrants for *mucosa*, etc. Finally, although the useless noun is retained in *dura mater spinalis* and *filum durae matris spinalis*, the very next terms in their list, *cavum epidurale* and *cavum subdurale*, are indirect and probably unintended, yet none the less complete, precedents for *dura* pure and simple, and for the substantive employment of any and all feminine adjectives whatsoever.

Epiphysis vs. *corpus pineale*. — His regards *epiphysis* as a "generelles Wort" ('95, 163), and the ancient dionym is adopted by the German committee.[2] My own earlier preference was for *conarium*, as already stated (p. 124). I now realize the desirability of the verbal as well as the topographic correlation with *hypophysis* and *paraphysis*, and the inutility of maintaining in all cases the rigid doctrine of 1871.

Fissura Centralis vs. *sulcus centralis* (or *fissura* or *sulcus Rolando*). — By comparison of the three columns it will be seen that two distinct points are concerned, involving respectively the generic and the specific names of this feature of the lateral aspect of the cerebrum. If eponyms or personal names are to be abandoned, as decided by the German committee and as advocated by me since 1880,[3] then all the derivatives of *Rolando* must be discarded in favor of *centralis* and its derivatives. Those who prefer the eponym should show that Rolando's figure and description really merit such commemoration, and should be also at least consistent in the employment of derivatives. *Paracentralis*, *praecentralis*, and *postcentralis* have no other justification than topographic reference to *centralis;* yet

[1] In Foster's Medical Dictionary, *dura* and *pia*, *dural* and *pial*, are major headings, *dura mater* and *pia mater* being merely synonyms.

[2] In *Science*, July 17, 1896, p. 71, the date *1895* after *epiphysis* would indicate its adoption by the Germans. That was an error for which I must be held responsible, and which was corrected as soon as possible after it was noted.

[3] With the exception of *fissura Sylvii* and certain derivatives of *sylviana*.

it is by no means uncommon to find in one and the same paper "fissure of Rolando" and "paracentral lobule."

As to the generic terms *fissura* and *sulcus*, the former has been consistently employed by me since 1880 for all linear depressions of the cerebral surface, while the German committee restrict it to the sylvian (called by them *cerebri lateralis*), the collateral, the occipital (their parieto-occipitalis), the calcarine, and the hippocampal, and name all the others *sulci*. They regard the striatum as constituting an ental correlative of the sylvian (p. 170); hence it may be inferred that *fissura* indicates a corrugation of the entire parietes, while *sulcus* indicates a linear furrow not represented in the cavity by a corresponding elevation.[1] Fully conceding the desirability of recognizing the distinction between the two groups of cerebral furrows, the following considerations lead me to question the advisability of employing the two generic words in the senses proposed by the German committee.

1. *Fissura* and its various paronyms and heteronyms are already well established and commonly associated with cerebral topography. This subject, on account of its various relations, physiologic, pathologic, surgical, and psychologic, has already gained much general interest. *Sulcus* is a comparatively unfamiliar word. It is distinctively Latin and technical. Its Latin plural, *sulci*, is even more so. It does not readily lend itself to paronymization, *sulc* and *sulcuses* both being somewhat unacceptable.

2. *Sulcus* has recently been employed by Mrs. Gage ('93), O. D. Humphrey ('94), P. A. Fish ('94), and B. F. Kingsbury ('95) for ental (entocelian or intraventricular) depressions which are less likely than the cerebral furrows to become subjects of general interest.

3. There is a practical difficulty that cannot be ignored. Nothing in the words *fissura* and *sulcus*, or in their ordinary associations, serves to admonish us as to the proposed distinction. Hence there is liability to misuse and confusion. Many

[1] The two groups are sometimes distinguished as *total* and *partial*, or as *complete* and *incomplete*. The former seem to be preferable, since with the total the totality of the parietes is involved, whereas *complete* and *incomplete* seem to imply differing degrees of perfection.

actual instances of this might be cited, but the following may suffice. Edinger ('95) apparently intends to apply *fissura* to the total fissures, and the occipital is so designated in the index; but on Fig. 33 it is called *sulcus*. Kölliker (*Entwickelungsgeschichte*, p. 555) attributes *sulcus calcarinus* to Huxley, who uses *fissure* as does Kölliker in the explanation of a figure. Flower ("Proteles," *Zoöl. Soc. Proc.*, 1869) applies to the supra-orbital, *fissura* and *sulcus* indifferently. Huxley (*Vertebrated Animals*) says that the cerebral surface becomes complicated by ridges and furrows, "the gyri and sulci"; but the first of the "sulci" to be mentioned is the "sylvian fissure," and the second "the fissure of Rolando," the latter also being designated on Fig. 21 as the "sulcus of Rolando." Flower and Lydekker (*Mammals*, p. 71) say "the sylvian fissure" is one of the most constant of the sulci. In the last two cases the generic designation of the shallower furrows is made to include both kinds, and, curiously enough, this usage is apparently sanctioned by the German committee in introducing *gyri cerebri* and *sulci cerebri* as comprehensive names, and then specifying certain sulci and fissurae.

Dentatum vs. *nucleus dentatus*. — Two separate questions are involved in the choice between these terms: (*a*) The use of *nucleus* (with a masculine adjective) in place of *corpus* (with a neuter); (*b*) The employment of an adjective of either gender as a substantive. The latter is considered in connection with *callosum* and *dura* (pp. 138–139). The substitution of *nucleus* for *corpus* seems to the American committee to constitute a step backward, as tending to obscure the commonly accepted distinction between the part in question, with the analogous part in the oliva on the one hand, and the "nuclei"[1] of origin of the various nerves on the other.

Falx vs. *falx cerebri*. — The German committee designate the slighter fold of dura between the two lateral masses of the cerebellum as *falx cerebelli*. The present writer prefers the diminutive, *falcula*. The American committee has not yet passed upon this case. Even should they retain *falx cerebelli*,

[1] The question of preference between *nucleus*, and *nidus* (Spitzka), and *nidulus* (C. L. Herrick) need not be considered upon the present occasion.

it would not prove a serious burden, because the part is hardly mentioned once while the cerebral septum is named ten times.

TENTORIUM vs. *tentorium cerebelli.* — This case is even stronger than that of falx, for tentorium is an idionym.

STRIATUM vs. *corpus striatum.* — See *callosum.*

CORNU DORSALE vs. *columna* (*grisea*) *posterior.* — Two distinct issues are involved here: (*a*) toponymic, between *posterior* and *dorsalis;* (*b*) organonymic, between *columna* and *cornu.* The former will be considered in connection with *cornu ventrale* and *radix dorsalis.*

CORNU vs. *columna.* — It is almost embarrassing to find myself advocating the maintenance of ancient and general usage against one comparatively novel. Probably most anatomic teachers will sympathize with the German committee in their objection to the application of *cornu* to what is really one of several ridges of a deeply fluted column of gray nervous tissue constituting the core of the "spinal cord"; ridges that resemble "horns" only when artificially exposed upon transection. At least ten years ago I was so deeply impressed by this inappropriateness of *cornu* as to hunt up an architectural term, namely, *arris*, signifying the ridge between two adjoining channels of a Doric column. Whether or not it was derived from *arista*, it is excellent Latin in form, and acceptable in every respect save its novelty.

Yet I believe that I did well to refrain from its introduction; for, after all, in nine cases out of ten the artificial appearance presented upon section is what is first offered the student, and I have never known a case of misapprehension occasioned thereby. Upon the whole, this has seemed to the American committee a good case for the observance of Huxley's aphorism ('80, 16) as to the unadvisability of interfering with terms that are well established and have a definite connotation, even when they may be etymologically inadequate, *c.g., callosum.* Individually, I should feel that the case against *cornu* would be much stronger were it a word of half a dozen syllables or lacking in euphony.

The assignment of *columna* to the ridges of the myelic cinerea naturally involved the replacement of that word as

commonly applied to the intervening masses of alba by some other word; the German committee selected *funiculus*. If *cornu* be retained, *columna* will be available as hitherto. Even if a change be made, however, why not *funis* instead of the longer diminutive, upon the grounds stated on p. 110? There could hardly be confusion with the same word as applied to the "umbilical cord."

Cornu Ventrale. — As an objection to this term it might be urged that consistency would involve the application of the same words to the "middle" or "descending" extension of the "lateral ventricle," which the German committee call *cornu inferius*. What the American committee may do in this connection remains to be seen. There would be no real cause for ambiguity, however, since *cornu temporale*, *c. frontale*, and *c. occipitale* are perfect examples of a class of terms that suggest parts or regions already familiar. Personally, I have never had any difficulty, the locative, mononymic idionyms (pp. 113, 150), *medicornu*, *praecornu*, and *postcornu*, having been consistently employed by me for fifteen years ('81b, d).

Radix Dorsalis vs. *radix posterior.* — Since, with this and with *radix ventralis* (or *anterior*) the Americans and the Germans are at one as to the substantive element, there only recurs the toponymic difference already alluded to in connection with the ridges of the myelic cinerea. The difference is far reaching and literally radical. As with the myelic sulci, columns, cornua, and commissures, the folds of the axilla, the aspects of the thigh, the tubercles of the cervical vertebrae, the sides of the stomach and other viscera, the valves of the heart, there is exemplified one of the most undesirable features of the pernicious influence of anthropotomy upon anatomy at large.[1]

Upon this subject the position of the German committee in 1895 is indicated by the following translation of passages from His ('95, 109, 110): "As mentioned above, Herr von Kölliker has proposed replacing generally the words *anterior* and *pos-*

[1] "The influence of the nomenclature of human anatomy, reflected downward upon the dawning structures of the lower animals which culminate in man, is nowhere more obstructive to a plain and true indication of the nature of parts than in regard to those of the brain." Owen ('61), I, 294, note.

terior by *ventralis* and *dorsalis* where the relations to comparative anatomy, and especially to the anatomy of domesticated animals, render it desirable; that is, where the terms *anterior* and *posterior* apply only to the upright attitude of man. . . . We do not deny the merit of such strict usage, but the commission has not been able to decide upon its adoption. It involves all kinds of difficulties and inconveniences. . . . We leave time to determine whether or not we shall depart from the traditional usage associated with the erect attitude of man."

Had most of the members of the commission been investigators and teachers of zoötomy rather than of anthropotomy, there would probably have been no hesitation in adopting terms that apply equally well to all vertebrates in any attitude. Let us hope that the distinguished president of the commission may live to see his recommendations unanimously adopted.

I close this discussion of the differences between the recommendations of the American and German committees with the remark that, strictly speaking, not one of the words in the first column of Table II can be imputed to us. All were in use for longer or shorter periods prior to 1880. Comparison with the second and third columns will show that in most cases our office was merely to disencumber the essential elements of preëxisting terms from superfluous accessories.

Criticisms of the efforts and propositions of the American committees in general and of myself in particular have been published by the Anatomische Gesellschaft,[1] by Professor Wilhelm His (see p. 110) and by Professor Kölliker.[2]

In these criticisms it appears that the Germans are at last[3]

[1] *Anatomischer Anzeiger*, Ergänzungsheft, 1895, p. 162.

[2] Gewebelehre, 6th ed., II, p. 814, 1896.

[3] I say "at last" in view of the enormous number of lengthy terms, both Latin and vernacular, for whose continuance and even origin German anatomists are responsible (p. 122). Some of the heteronyms are indeed "fearfully and wonderfully made," and can be most fitly characterized as verbal "tandems," unmanageable by persons not specially trained. As remarked by Owen, "The happy facility for combination which the German language enjoys has long enabled the very eminent anatomists of that intellectual part of Europe to condense the definitions of anthropotomy into single words; but these combinations cannot

in accord with the Americans in recognizing the value of brevity as a feature of anatomic terms. But I have as yet failed to find in their publications or private letters even the faintest glimmer of comprehension of the two-fold superiority of mononyms (single-word terms) over polyonyms (terms of two or more words), *viz.*, their capacity for (*a*) inflection, and (*b*) adoption into other languages with little or no change of form.

In order to eliminate so far as possible the personal element from the consideration of the special criticisms of Professor His, I select as the first subject of rejoinder a term, *postcava*, in which my interest is only indirect, as of one toward a child by adoption rather than by paternity. Omitting intervening phrases not affecting the interpretation, the complaint of Professor His reads (translated) as follows: "Wilder and his colleagues . . . say *praecornu* and *postcornu* for *cornu anterius* and *cornu posterius*, *postcava* for *vena cava posterior*, with many similar terms." The accompanying implied disclaimer as to "philologic pedantry" can hardly embrace a toleration of misstatement; hence, before discussing the intrinsic merits of the word selected, it may be well to dispose of minor points that might complicate the main issue.

In the text Professor His refers only to "Wilder," and in note 2 an initial is wrong. Hence it is only just to state that my terminologic transgressions must not be imputed to Harris H. Wilder, professor in Smith College, Northampton, Mass., whose researches, especially upon lungless salamanders,[1] make me proud to claim him as a distant relative.

The objectionable words are attributed to "Wilder and his colleagues." Not one of the three specified words or of the "many similar terms" has been sanctioned by either of the four committees, and few of the members thereof have adopted them. For the confusion and possible injustice here occasioned no adequate explanation can be offered.

The phrase, "postcava statt vena cava posterior," would

become cosmopolitan; such terms as 'Zwischenkiemendeckelstück' are likely to be restricted to the anatomists of the country where the vocal powers are trained from infancy to their utterance."

[1] *Anatomischer Anzeiger*, IX, Jan. 20, 1894, and XII, 182–192, 1896.

naturally imply that the latter is the name preferred by the German committee. Yet the official list contains (p. 77) only *vena cava inferior*.[1]

So far as appears in the article of Professor His, *postcava* was coined by me. On the contrary, so far as I am aware, it (in the derivative *postcaval*) was first introduced by Richard Owen about the middle of the century, and employed by him consistently thereafter.

Whether or not the two historic facts just mentioned[2] were known to Professor His he alone can tell, and the fate of other queries does not encourage an effort to ascertain. Hence I am compelled to offer propositions which each reader must accept or reject in accordance with his own information and judgment.

1. *Postcava*, in the form *postcaval*, occurs frequently in the writings of a leading English anatomist.

2. Those writings must be known and accessible to Professor His. Hence there is no excuse for the erroneous intimation in the article.

3. Whatever its source, *postcava* differs from the more usual terms in its comparative brevity, while at the same time it is not open to the charge of ambiguity. Why, then, was it not included in the column of synonyms from "sonstigen Autoren" in the protocols of the German committee, as was a less common and acceptable synonym, *viz.*, "vena cava inferior thoracica?"

4. If the entire committee supposed me to be the author of *postcava*, their action was consistent, since no term is credited to me in the column indicated.

5. But if any members of the committee knew that *postcava* originated with Richard Owen, their objections to the word might well have been waived out of respect for him.

The actual form employed by Owen is specified above, not merely for the sake of accuracy, but also in order to forestall criticism upon a point where disagreement is possible. It is,

[1] In passing it may be remarked that the retention of *superior* and *inferior* as the essential elements of the designations of these great vessels constitutes one of the many evidences of the non-emancipation of the German committee from anthropotomic enslavement (see p. 144).

[2] My non-responsibility is certain; the responsibility of Owen is assumed in the absence of evidence to the contrary.

I think, a sound proposition that *the introduction of any derivative, oblique case, or national paronym practically renders the introducer responsible for the actual or potential Latin antecedent of such words, in accordance with the usual rules of derivation and paronymy.* I do not remember seeing the foregoing proposition distinctly formulated,[1] but reflection will show its soundness. One of the wisest recommendations of the A. A. A. S. Committee on Biological Nomenclature (p. 130) was that the Latin (international) form of a term should always be given, whether or not the national paronyms. Now *cava* is the feminine form of *cavus*, and *vena cava* was used (perhaps not in the specific modern sense) by Cicero, *De Natura Deorum*, 2, 55, 38.[2] There seems to have been no classic adjective, although *cavatus*, the particle of *cavo*, was available as such. Analogy fully warrants (pp. 139 *et seq.*) the acceptance of *cava* as a substantive, and the derivation therefrom of a secondary adjective in the form of either *cavatus* or *cavalis*. The latter evidently was chosen (constructively) by Owen when (in 1862, "On the Aye-Aye," *Zoöl. Trans.*, V, 86, and perhaps earlier) he employed *post-caval vein* and *pre-caval vein*. Later the hyphen was omitted, and in the *Comparative Anatomy of Vertebrates* occur "postcaval vein, postcaval trunk, postcaval orifice, and postcaval," I, 503–505; II, 203; III, 552 *et seq.* Pending the discovery in Owen's writings of some history of the stages by which the final reduction was effected, the following series is certainly thinkable: (1) Vena cava posterior, (2) Posterior vena cava, (3) Posterior caval vein, (4) Post. caval vein, (5) Postcaval vein, (6) Postcaval vein, (7) Postcaval, (8) Postcava. Whatever may have been the actual steps, never did Owen reach a more commendable terminologic result, and no case better exemplifies the unwisdom of the reactionary attitude of the German committee.

Since Professor His offers no specific objections to *postcava*, their nature can only be inferred from his general remarks and

[1] It probably has been in purely linguistic connections. My suggestion that the principle apply likewise to zoölogic names ("Amphibia or Batrachia," *Science*, Aug. 20, 1897, p. 295) has been repelled with a needless asperity (*Science*, Sept. 3, pp. 372–373).

[2] For some discussion of *cava* see Hyrtl, ('**80**), 98, 99.

from his criticisms of *medipedunculus*. Perhaps, therefore, the simplest and most comprehensive rejoinder is to recapitulate briefly the several attributes of the term, leaving each reader to estimate their value for himself.

(*a*) Brevity. (*b*) Latin form. (*c*) It is a mononym. (*d*) It is a locative name. (*e*) It is an adjectival locative. (*f*) It is capable of inflection; *i.e.*, *postcavalis*, *postcaval*, *postcavals*. (*g*) Its various national representatives (paronyms, p. 117) differ little or none from the international antecedent. (*h*) It has in the derivative, *postcaval*, high authority (Richard Owen) and moderate antiquity (1862 or earlier). (*i*) It is an idionym, and not likely to be applied to any other part in any vertebrate. (*k*) It is sufficiently euphonious, and easily remembered. (*l*) Like other euphonious and easily remembered mononyms it constitutes no bar to the progress of one who may never have heard the more common polyonyms. Those who are familiar with those polyonyms, whether *vena cava inferior*, *vena cava ascendens*, or *vena cava posterior*, could hardly fail to recognize its signification. Since 1881 no other term than *postcava* has been used by me for the great vein in question. I have yet to learn of a single instance of misapprehension or other difficulty caused thereby among either general or special students.

There remains the question of the etymologic orthodoxy of *postcava*, and this involves the much more comprehensive and difficult question as to the definition of etymologic orthodoxy. Without presuming to invade the jurisdiction of philologic experts, for the practical discussion of the case in point precedents need be sought in only two periods, the classic and the recent.

I freely admit that there is known to me no instance in classic Latin literature of the employment of *post*, whether alone or in composition, with the force of an adjective and as equivalent to *posterus* or *posterior*. That this negative evidence is hardly conclusive may be seen from a single case among the scores that might be adduced. With the Romans *item* was an adverb. With us it is not only an adverb, but also a noun and a verb, and the basis of two derivatives, *itemize* and *itemizer*.

In recent times the precedents are partly direct and partly indirect. Among the former are *postabdomen*, *postact*, *postarytenoid*, *postfactor*, *postfurca*, *postpubis*, *postscapula*. In all of these *post* has the force of an adjective, not of a preposition.

Indirect precedents are cases in which other prepositions have the force of adjectives in composition. Such are *preadaptation*, *precentor*, *preëxistence*, *preformation*, *presternum;* also *subgenus*, *subflavor*, *subfactor*, *submaster*, *subtitle*.[1]

Since, however, the German committee sanction none of the anatomic terms in the foregoing lists, and avoid the use of *praesternum* by retaining *manubrium sterni*, they would probably decline to regard them as adequate justifications for *postcava*. But can they consistently condemn it or any similar terms? Let us see.

Professor His, the German committee, and the Anatomische Gesellschaft, after several years' deliberation, and apparently without any disagreement, have adopted and recommended the names *metencephalon* and *prosencephalon* for certain segments of the brain. Now *meta* and *pros* are the English forms of the Greek μετά and πρός. These are both prepositions. Like *post* and *prae* they are also adverbs. The terms into which they enter have no reference to a third part "behind" which or "before" which the metencephal and prosencephal are situated. The German translation of *prosencephalon* is *Vorderhirn*, and the English, *forebrain*, both signifying the first or most cephalic member of the series of coördinate encephalic segments. With slight modifications the foregoing remarks apply equally to a third name adopted by the German committee, *diencephalon*, the preposition διά having the force of an adjective.

I am unable to recognize any distinction, logical or etymological, between the *metencephalon* and *prosencephalon* which the Germans commend and the *postcava* and *praecava* which Professor His condemns. The irregular terms for which he is in part responsible may be few; but his virtuous denunciation

[1] Among analogous Greek words the following has been furnished me by my friend, L. L. Forman, instructor in Greek at Cornell University: προφύλαξ, an advance guard.

of me for producing a larger number of the same sort is no more reasonable than the demand of the woman to be punished lightly for bringing forth an illegitimate child upon the ground that it was "such a little one."

Strictly, however, even if the degree of opprobrium to be cast upon the individual concerned were to be measured by the number of terms of a certain kind, this would have no bearing upon the question of the acceptability of a given term. *Postcava* and *praecava* are to be considered upon their merits as brief, convenient, and absolutely unambiguous designations intended to replace inconvenient descriptive phrases. In favor of *vena cava superior* and *vena cava inferior* antiquity alone can be urged; against *praecava* and *postcava* can be alleged only the sinfulness of comparative youth.

In the foregoing discussion I have refrained from following one line of argument that readily suggests itself and is, indeed, almost formulated in the hypothetic series between *posterior vena cava* and *postcava*, as stated on p. 148, *viz.*, the prefix *post* might not unnaturally be regarded as the abbreviation of *posterior* or *postero*. Were compounds of *post* alone concerned, this simple line of argument might, perhaps, be adequate; but it will not serve for compounds of the correlative *prae*, nor for those of the Greek prepositions, ἐπί, μετά, ὑπό, etc.

The straightforward way of dealing with the matter is to assume that *post* and *prae*, in composition, may have the force of the adjectives *posterior* and *anterior* respectively.[1] "If this be treason, make the most of it."

It seems to me that the nature of the issue between *postcava* and *vena cava inferior* (or *posterior*) is such as to involve the acceptance or rejection of the following propositions:

(*a*) Language was made by and for man, and not the reverse.

(*b*) Grammatic rules are framed from time to time in order to maintain the uniformity that is acceptable and convenient.

[1] It is well understood in this country that the *New York Medical Journal* and the Encyclopaedic Medical Dictionary stand for the highest scholarship. Yet so long ago as 1885, when some of my simplified terms were submitted to him, their editor, Dr. F. P. Foster, replied: "I think some of the words excellent, *praecommissura*, for example."

(*c*) Like the roads we traverse, such rules are but means to ends, and have no intrinsic sanctity.

(*d*) Like a circuitous but familiar road, a commonly accepted rule is not to be abandoned without reflection. On the other hand, no more is it to be laboriously traveled when new conditions render a "short cut" desirable.

(*e*) Extrinsic toponyms (that is, terms of location or direction that do not refer expressly to the recognized body-regions, dorsum, venter, etc.) should conform to the more usual vertebrate attitude rather than to the erect attitude of man; *e.g.*, *posterior* and *anterior*, *superior* and *inferior*, and their derivatives, compounds, and abbreviations should have significations zoötomic rather than anthropotomic.

(*f*) There now prevail and are likely to persist two conditions not merely unknown to the *Patres anatomici*, but probably not imagined by them: (*a*) the enormous increase of anatomic and physiologic knowledge; (*b*) its general diffusion among the people.[1] These two conditions[2] militate against the rigid maintenance of grammatic rules that might prevent the establishment of new and shorter channels, or the fabrication of new and briefer technical terms, the "tools of thought." Terms like *vena cava posterior* are obtrusively Latin, and hence not acceptable to the laity; too much time and space are lost in speaking and writing them, and time and space are daily becoming more precious.

Consciously or unconsciously, for many years English and American anatomists have been gradually simplifying their terminology in substantial accordance with the foregoing propositions. In Germany the signs of such improvements are as yet comparatively few.

Even if, however, the German committee were reconciled to

[1] In fulfillment of the declaration of the elder Agassiz, "Science must cease to be the property of the few; it must be woven into the common life of the world."

[2] There is really a third condition, equally novel, but bearing less directly upon the present question, *viz.*, the pursuit of anatomy by women. Whatever view may be taken of this in other respects, all decent men must rejoice that it has hastened the elimination of the needless *Nomina impudica* which formerly defiled even the description of the brain. For further commentary upon this matter see W. & G., ('**82**), 27.

the employment of certain prepositions in composition with the force of adjectives, there would still remain [1] special objection to *post* as indicating toward the tail rather than toward the back. This objection is radical, and the conflict involved is irrepressible (pp. 144–145).

Postramus.— To this, as a mononymic substitute for *Ramus posterior arboris vitae cerebelli*, Professor His offers no specific objections, but they may be inferred to be (*a*) that it is a *post* compound (pp. 146–152); (*b*) that the German list does not include any terms for the branch-like divisions of the cerebellar "tree." If these branches no longer merit specification, *postramus* and *praeramus* will vanish quietly with the ancient polyonyms from which they were condensed.

Isthmus. — Professor His complains that this word is used by me in the sense of *Gyrus annectens.* This latter term does not occur in the German list, so I assume that *Gyrus transitivus* is meant. No one of my terminologic propositions gives me more satisfaction than that of replacing *Gyrus annectens*, *bridging convolution*, and *pli de passage*, by *isthmus*, when the cortical area is visible at the surface, and by *vadum* when it is concealed; the occasional interruption of the central fissure is thus the *Isthmus centralis;* that between the adjoining ends of the parietal and paroccipital fissures, the *Isthmus paroccipitalis*, etc. So far I cheerfully plead guilty to the charge. But with what justice does Professor His complain further that this employment of *isthmus* is in an "unusual sense" when his own list contains *Isthmus gyri fornicati?* Indeed, even were this complaint well founded, it comes with a poor grace from (*a*) a German whose fellow countryman (Waldeyer) applied (1891) to the nerve-cell the term *neuron*, which had been introduced by me ('84) for the entire cerebro-spinal axis; from (*b*) a member of the Nomenclatur Commission, whose chairman (Kölliker) applied (1893) to the axis cylinder process of a nerve-cell a term (*neuraxon*) practically identical with one (*neuraxis*) which occurs in a standard French medical dictionary for the cerebro-spinal axis; and from (*c*) one who himself, upon altogether inadequate grounds, has made the term in question, *isthmus*,

[1] Excepting with the chairman, p. 145.

of segmental value, and who has needlessly and unjustifiably modified the scope of *prosencephalon* and reversed the hitherto commonly accepted sense of *metencephalon*.

Medipedunculus.—To this term Professor His devotes one-fourth of his entire criticism. Hence some rejoinder should be made, although the objections impress me as either ill-founded in themselves or inconsistent upon the part of the objector. As a word *medipedunculus* is no more "barbarous" than *meditullium*, *Mediterranean*, or *medieval*. As a designation rather than a description, it requires definition. The beginner would remember *medipedunculus* quite as easily as "pedunculus cerebelli ad pontem";[1] and since experienced anatomists know that there are three cerebellar "stalks" on each side, but only two "pedunculi cerebri," one on each side, he is not likely to infer that either of the latter is meant by *medipedunculus*. In fact, this term, as coined and defined by me,[2] is now an idionym, applicable to but a single part of the brain.

In order to be absolutely explicit and independent of the context, the following terms from the German list should be accompanied by the words here bracketed after them: *Clivus* [*occipitalis*], *Clivus* [*sphenoidalis*], *Pars cervicalis* [*medullae spinalis*], *Sulcus lateralis anterior* [*medullae oblongatae*], *Sulcus limitans ventriculorum* [*encephali*], *Pars centralis* [*ventriculi lateralis*], *Ventriculus terminalis* [*medullae spinalis*], *Lamina terminalis* [*encephali*]. The identity of the adjective in the last two terms would lead the beginner to associate them topographically, and he certainly would never infer that they designate parts at opposite poles of the cerebro-spinal axis.[3]

From the standpoint of Professor His the foregoing must be regarded as serious blemishes upon the German list. From

[1] This term, by the way, does not occur in the German list, where apparently it is replaced by *brachium pontis*.

[2] In this connection two remarks are naturally suggested: (1) *Medipedunculus* is an adjectival locative, it and its correlatives, *praepedunculus* and *postpedunculus*, constituting one of the most perfect groups of that kind (pp. 113–114); (2) the obtrusively Latin termination of these words, as well as the length of the words themselves, forced upon me in 1884 (p. 122) the consideration of the whole subject of paronymy.

[3] In the absence of adequate context or prior definition, would any reader imagine that *spongiocyte* and *spongioplasm* refer to elements of the nervous tissue?

my point of view, although I might object to certain of the names as such, it would not be on account of their lack of explicitness. As has been said above, in many instances explicitness is to be gained from the context. But with really the larger number, I am confident that well-selected, brief, and fairly suggestive designatory names can and will be learned and remembered without any difficulty, especially if the study of the brain be begun at an early age.

Coelia. — This word, in place of *cavitas encephali s. ventriculus encephali*, is one of the three enumerated by Professor His as examples of my many terms that are objectionable because they are "new." In the lexicon of Liddell and Scott κοιλία ἐγκεφάλου is quoted as in good and regular standing among Greek medical writers. According to Burdach (*vom Baue und Leben des Gehirns*, 1819–22, II, 301, 378, 380), Galen designated the "fourth ventricle" as κοιλία ὀπισθίου ἐγκεφάλου, τετάρτη κοιλία and ὀπισθία κοιλία (*De usu partium*, Lib. VIII, CXII, p. 170); the "third ventricle" as μέση τρίτη κοιλία (*idem.*, IX, III, 172); and the "lateral ventricles" as προσθίαι κοιλίαι (*De odoratus instrumento*, II, 110). *Coelia* is then certainly not "new." Had Professor His said *unusual*, his objection would have been more nearly justified by the facts, although in recent encephalic literature on both sides of the water compounds of *coelia* are more and more frequently encountered.

In favor of *coelia* (English *celia* or *cele*) in place of *ventriculus* may be urged the following:

(1) Its Greek origin renders it compoundable regularly and euphoniously with the characteristic prefixes already employed in the segmental names, *e.g.*, *mesencephalon*, etc.

(2) These compounds are mononyms, and therefore capable (p. 118) of inflection (*e.g.*, *mesocoeliae*), derivation (*e.g.*, *mesocoeliana*), and adoption into other languages without material change; *e.g.*, English, *mesocele;* French, *mesocoelie;* German, *Mesokölie;* Italian, *mesocelia.*

(3) The various national paronyms thus formed are likewise capable of derivation; *e.g.*, *mesocelian.*

(4) There is classic authority for the use of *coelia* in the sense of encephalic cavity (see above).

(5) These ancient usages are assumed to be familiar to educated anatomists, who therefore should recognize the compounds with little or no hesitation.

(6) The compounds are so euphonious and so obviously correlated with the segmental names as to be learned and remembered easily even by general students and by those who may not have had a classical training.[1]

(7) In recent times it has been independently proposed by two anatomists, teachers as well as investigators.[2]

(8) It has been adopted more or less completely by three of the older American neurologists, Henry F. Osborn ('82, '84, '88), E. C. Spitzka ('81, '84), and R. Ramsay Wright ('84, '85), and unreservedly by eight of the younger, W. Browning, T. E. Clark, P. A. Fish, Mrs. S. P. Gage, O. D. Humphrey, B. F. Kingsbury, T. B. Stowell, and B. B. Stroud.

It will be noted that among the advantages of *coelia* over *ventriculus* is not enumerated its freedom from ambiguity. Theoretically, of course, *ventriculus* (*encephali*) might be mistaken for *ventriculus* (*cardiae s. cordis*). Practically, however, the context would almost infallibly obviate misapprehension.[3] Hence, from my point of view, the absolute unambiguity of *coelia* and its compounds would not in itself justify its replacement of *ventriculus*. It would be a *causa vera*, but hardly a *causa sufficiens*.

The concluding remark of Professor His may be said to "cap the climax" of his ill-founded criticism. The characterizations, "völlig neuen" and "grossentheils recht fremdartig

[1] Among the hundreds of such students at Cornell University and at the Medical School of Maine who have gained their practical and theoretic knowledge of encephalic morphology by means of these compounds no special difficulty has ever been experienced.

[2] My propositions first appeared in *Science*, March 19 and 26, 1881. On the fifteenth of August, 1882, Prof. T. Jeffery Parker read before the Otago Institute of New Zealand a paper ('82) in which *mesocoele* and similar compounds were introduced, although he was evidently quite unaware of my prior publication. The terms were also employed in his "Zoötomy" ('84) and in a later paper ('86).

[3] My previous reference to the polyonymic derivative, *sulcus limitans ventriculorum*, was not for the sake of demonstrating the ambiguity of that term, but to illustrate the inconsistency of the implied demand of Professor His that all terms must be self-explanatory and require no definition.

Klingenden," could hardly have been more sweeping had I proposed to replace Latin by Choctaw. Any anatomist, unprejudiced and not above conceding the possibility that some good thing may come out of the American Nazareth, who will candidly compare the terms in Table VI (Part VII) will admit that in the second column a comparatively small number are new in the strict sense of the word, and that the large majority are either identical with those in the first, or differ therefrom merely in the omission of useless words, or in the replacement of adjectives by prefixes of like signification.[1]

Among the special terms to which objection is expressed by Professor Kölliker are *aula* and *proton*, and they are here briefly defended.

Aula. — After years of confusion, doubt, and even distress of mind, induced by the failure to reconcile the facts of development and comparative anatomy with the prevalent nomenclature of the brain in 1880 ('80d, e, f; '81b, d), I proposed *aula* upon grounds formulated two years later as follows (W. and G., '82, § 1065):

(1) To substitute brief single words for the phrases "ventriculus communis," "ventriculus lobi communis," mesal part of the "common ventricular cavity," "foramen Monroi," etc.

(2) Because the phrase most commonly employed, *foramen Monroi*, is used to designate at least three different cavities or orifices: (*a*) the cavity by which either paracoelia ["lateral ventricle"] communicates with the mesal series of cavities; (*b*) the two lateral orifices together with the intervening space; (*c*) the mesal [cephalic] orifice of the diacoelia. We have been unable to ascertain by whom the phrase was first employed, and the description by Munro *secundus* (**1783**), in whose honor it was applied, is somewhat vague.

(3) In order to indicate our opinion of the desirability of recognizing the aula as morphologically an important element of the series of encephalic cavities.[2]

[1] At that time, although my principal article on terminology had not been read by Professor His (see Part VI), the lists of terms preferred by me were in his hands, so that no claim can be entertained that he referred merely to what he assumed my proposals "tended" to bring about.

[2] With some of the lower vertebrates (*e.g.*, *Chimaera*, '**77a**), the aula is much more extensive than either of the "lateral ventricles" with which it is connected through the two portae.

Proton. — This neuter noun was used by me ('93a, § 46, note) to designate the comparatively undifferentiated mass in which two or more parts might afterward be distinguishable. It is free from certain obvious and by no means inconsiderable objections that may be brought against *Anlage* and *fundament* as English words. It is subject to inflection, and may be adopted into any language. In many derivatives or compounds it is associated in the minds of all educated persons with the general idea of primitiveness. Its employment is in harmony with the following phrases from Aristotle cited for me by Prof. B. I. Wheeler: τὸ πρῶτον, ἡ πρώτη ὕλη, ἡ πρώτη αἰτία.

In short, all my regrets for the errors already confessed (p. 125) and for others of which I may be convicted, together with all my doubts regarding certain of the terms not as yet acted upon by the American committees, shrink into the background of my mind as I reflect upon the nature and significance of *aula* and *proton*, and upon the advantages that have been and may be gained from their employment.

Apparently, also, Professor Kölliker objects to hybrid words as "Barbarismen." Yet the German list, adopted by a committee of which he was chairman, contains at least fourteen compounds of Greek and Latin elements, *viz.*, *epi*durale, *meso*varicus, *par*umbilicales, *par*olfactorius, peri*chorioidiale*, supra*chorioidea*, *chorio*capillaris, *pterygo*palatinus, *pterygo*mandibularis, *phrenico*costalis, *spheno*palatinum, *spheno*occipitalis, occipito*mastoidea*, and squamoso*mastoidea*.

The reasonable view of hybrid terms seems to me to be embodied in the following remark of Barclay in 1803:

> "Notwithstanding the opprobrium attached by some to certain connections and intermarriages among harmless vocables, I should be inclined not to reject the coöperation of the two languages (Greek and Latin) where experience shows it to be convenient, useful, or necessary."

Abstractly, we may all prefer horses to mules, but this need not hinder us from recognizing that, under certain circumstances, the latter are more efficient than the former, and that, in a given case, a horse may not be even so handsome as a mule.

The verdict of Professor Kölliker that the nomenclature coming from America in recent years is a "complete failure" because he cannot read the articles based thereon approximates what has been called "the erection of the limitations of one's individual experience into objective laws of the universe." I sincerely trust that he may some day concede the validity of these two propositions: (1) A considerable number of investigators and advanced instructors on both sides of the ocean have employed the "American" system more or less systematically. (2) Judging from my own experience as learner and teacher, the hundreds of students, general and special, upon whom that system has been practised since 1880 have either saved so much time or gained so much more information within a given time as to make its employment "worth while," even when the later environment proved unfavorable to its permanent use.

In concluding this response to the criticism of "the oldest German anatomist," I venture to call his attention to the different reception accorded my plans for terminologic simplification by two other anatomic teachers well advanced in years, *viz.*, Joseph Leidy (p. 121, note) and Oliver Wendell Holmes (p. 127). In order, also, that I may not appear unmindful of the fact that the assimilation of verbal novelties becomes less easy with increasing age,[1] I reproduce the concluding paragraph of my second paper upon the subject ('81b):

> The beginner can learn the new terms even more easily than the old, and at any rate he has nothing to forget. But the trained anatomist shrinks from an unfamiliar word as from an unworn boot; the trials of his own pupilage are but vaguely remembered; each day there seems more to be done, and less time in which to do it; nor is it to be expected that he will be attracted spontaneously toward the con-

[1] The *tu quoque* argument is ungracious at the best, and the occasions for its employment in this paper have been too numerous already. But when I recall the delay and mystification inflicted upon me and my students by the variety and heterogeneity of terms, Latin and vernacular, with which most German treatises upon encephalic anatomy literally bristle, I cannot but feel that, however sincere may be the repentance therefor among the anatomists of that nation, the needed reform should have been practised for a somewhat longer period before others were rebuked.

sideration that his own personal convenience and preferences, and even those of all his distinguished contemporaries, should be held of little moment as compared with the advantages which reform may insure to the vastly more numerous anatomical workers of the future.

Commentaries upon Table III.

Its purpose is twofold: (*a*) to indicate, according to my present information and belief, the number and constitution of the definitive encephalic segments; (*b*) to illustrate the verbal correlations between the names of the segments themselves (column 2), and those of (3) their major cavities, (4) their membranous parietes, and (5) their vascular plexuses.

It is in some respects an amplification of the table on page 409 in W. and G. ('82). It differs from that in my later paper ('89a, 121) in (*a*) the recognition of the rhinencephal, and (*b*) the vertical arrangement of the segments.

From Schwalbe's table ('81, 397) it differs mainly in the absence of any attempt to indicate the relative "values" of the several segments upon embryologic or other grounds.

In this respect it differs also from that of His ('95, 161). In this latter, moreover, I have not as yet succeeded in recognizing consistency with (*a*) his other table on page 158; (*b*) the segmental arrangement employed in the German list of neural terms (80–87); (*c*) a discriminating use of terms; (*d*) due regard for precedent, or (*e*) the facts of comparative anatomy as I interpret them.

Conceding the high authority of Professor His as to the embryology of man, I nevertheless believe it to be altogether undesirable to infer the segmental constitution of the vertebrate brain from the conditions presented during the development of the human organ. Indeed, if the embryology of other forms were also taken into account, the number of potential "neuromeres" would be unmanageably large, even if any two investigators could agree at present as to how many should be recognized.

While anticipating that the problems involved will be eventually elucidated upon the basis of all the facts concerned, I

Table III.

Provisional Grouping of Some Neural Parts according to Their Segments and Some Other Characters.

	1. Chief Constituent	2. Segment	3. Cavity	4. Membranous Portion	5. Plexuses	6. Thin and Riparian Parts	7. Commissures, etc.	8. Some Other Parts
I	Bulbi olfactorii	Rhinencephalon	Rhinocoelia	Rhinotela (in some "fishes")			Praecommissura (pars olfactoria)	Praecribrum ; limen
II	Cerebrum	Prosencephalon	Prosocoelia (including the mesal aula and lateral paracoeliae)	Prosotela (including the mesal aulatela and lateral paratelae)	Prosoplexus (including the mesal auliplexus and lateral paraplexuses	Taenia ; fimbria ; pala ; terma	Praecommissura (pars temporalis); callosum ; fornix	Pallium ; insula ; lenticula ; caudatum ; paraphysis
III	Thalami	Diencephalon	Diacoelia	Diatela	Diaplexus	Habena	Supracommissura ; medicommissura ; chiasma	Postcribrum; tuber; hypophysis ; epiphysis ; genicula
IV	Quadrigeminum	Mesencephalon	Mesocoelia	Mesotela (in the lamprey)		Valvula	Postcommissura ; decussationes tegmentorum	Crus; tegmentum; crusta; lemniscus ; intercalatum
V	Cerebellum	Epencephalon	Epicoelia	Epitela	Epiplexus	Lingula	Pons	Praeoblongata ; vermis ; flocculus ; dentatum
VI	Postoblongata	Metencephalon	Metacoelia	Metatela	Metaplexus	Metaporus ; ligula ; obex	Decussatio pyramidum	Pyramis ; oliva ; trapezium
VII	Myelon	Myelon	Myelocoelia	Myelotela (in lumbar enlargement of birds)			Commissura ventralis ; c. dorsalis	Conus ; filum

believe our present effort should be to agree upon a *schema* of the vertebrate brain which, while not contravening the facts of embryology, shall harmonize so nearly with the facts of comparative anatomy as to facilitate rather than obstruct an effort to describe and interpret the conditions encountered in a given brain.

I freely admit my ignorance or non-comprehension of certain points, and also that my views have varied somewhat, particularly as to the segmental value of the olfactory region of the brain. Nevertheless, I regard myself as justified in advocating the *schema* presented above upon the following grounds: (1) for more than twenty years the general question has never been long out of my mind; (2) with special reference to it I have prepared and studied scores of brains of all classes and most of the orders; (3) the subject has been discussed more or less fully in papers by me upon the brains of many different forms; (4) papers upon other forms [1] have been prepared at this institution; (5) the *schema* has proved practically available for research, as indicated above, and has been readily comprehended and remembered by even general students.

What I advocate is that there be recognized for the present six definitive segments of the vertebrate brain under the titles Rhinencephalon, Prosencephalon, Diencephalon, Mesencephalon, Epencephalon,[2] and Metencephalon. It is my intention to review the whole subject at the coming meeting of the Association of American Anatomists in May, 1897.

Practical Suggestions. — As one of the older American anatomists, and as having committed at least my full share of terminologic errors, I venture to formulate some suggestions of a practical nature for the benefit of the younger generation.

Caution in Publishing New Terms. — It is true that words needlessly introduced into anatomy have no such embarrassing

[1] See papers by Clark, Mrs. Gage, Fish, Humphrey, Kingsbury, and Stroud.

[2] Even if Osborn is correct in his interpretation of the cerebellum as "primitively" intersegmental (**'88**, 57), he nevertheless admits that it "secondarily acquires a functional importance equal to that of the other segments." In *Science*, Sept. 3, 1897, p. 373, I have asked information as to the origin of these and other segmental names.

permanency as is conventionally assigned to synonyms in systematic zoölogy. Nevertheless, for a time, at least, they encumber current publications and dictionaries. Hence, however necessary and legitimate they may seem to the framer, neither a new term nor an old one in a new sense should be actually published without prolonged consideration, and consultation with at least four individuals representing as many categories of possible critics: (*a*) an investigator of the same general subject; (*b*) an experienced teacher; (*c*) an earnest student; (*d*) a philologic expert whose admiration for the past has not blinded him to the needs of the present and the future.

Method of Introduction of New Terms. — As "urgently recommended" by the A. A. A. S. Committee on Biological Nomenclature, "Whenever a technical word is used for the first time the author should give in a special note: (*a*) the Latin form; (*b*) the etymology; (*c*) the proper adopted form or paronym for his own language, with the adjective, etc., when applicable; (*d*) as concise and precise a definition as possible."

Indirect Responsibility for Latin Terms. — Even when the foregoing admirable rule is not followed, the validity of the following can hardly be questioned: "The introduction of any derivative, oblique case, or national paronym renders the introducer responsible for the actual or potential Latin antecedent of such word in accordance with the usual rules of derivation and paronymy (p. 148).

Paronyms vs. *Heteronyms.* — Excepting with a few conspicuous or particularly important parts, *e.g.*, head, heart, brain, etc., there should be employed either the Latin (international) names or the national paronyms. It is quite true that "calling a millstone by a Greek name does not enable us to see a whit farther into it"; yet the designation of parts of the body by terms of classic source, even if somewhat modified in form, enables the anatomists of other nationalities to apprehend the signification more readily than they might from vernacular words.

Homonyms. — As has been repeatedly observed (pp. 113, 144, 156), the context commonly averts misapprehension as to words having two or more meanings. The probability of confounding the mouth with a bone is scarcely greater than that

of mistaking a mathematic for a urinary calculus. But when a term or phrase possibly ambiguous is first introduced in a given publication, and especially in the title, absolute explicitness should be attained, no matter how many qualifying words may be required. In the title of a paper, the term "cervical follicles" is certainly ambiguous, and while "mental prominence," as employed by Huxley, is shown by the context to designate a projection in the region of the chin, in a title it might be readily misunderstood, particularly by a psychologist.[1]

Consistency. — This ranks second among the desirable attributes of all scientific writing which I have long called the five C's, *viz.*, Clearness, Consistency, Correctness, Conciseness, and Completeness. The last may seldom be attained; the lack of the first and second is as rarely excusable.[2] The practice of the virtue of terminologic consistency is tantamount to avoidance of the vice of pecilonymy.

Avoidance of Pecilonomy. — Whatever doubts a writer may entertain as to the relative excellence, authority, or vogue of two or more synonyms, and however he may shrink from committing himself to either one of them (p. 115), justice to his readers, if not regard for their good opinion, should lead him to make his selection in advance, and to adhere thereto throughout a given publication.[3]

Abbreviational Methods. — The following rules are recommended: —

[1] The title ("On the Fracture System of Joints, with Remarks on Certain Great Fractures") of a paper just received (*Bost. Soc. Nat. Hist. Proceedings*, XXVII) might at first sight seem to concern the surgeon quite as much as the geologist.

[2] While never really justifiable, obscurity of style may result from conditions more or less difficult to avoid; let us assume that no scientific writer would deliberately formulate the doctrine credited by Jules Janin to Balzac. When asked the meaning of a passage the novelist is reported to have replied: "Ceci pour le bourgeois," and to have explained that an unintelligible sentence or phrase now and then had a good effect on the "general reader," who, if the sense were always too obvious, might flatter himself that he was equal to the writer and on a level with his thoughts.

[3] As stated on p. 120, the principle and method were adopted by me in 1880. At that time Henle's works were not known to me. But in 1884 I was so impressed with his systematic employment of a single set of names that the first step in the collaboration toward Foster's Medical Dictionary (p. 121) consisted in photographing the "Index" of his "Nervenlehre" and distributing copies for discussion.

(*a*) The abbreviation should indicate the Latin (international) name. With all mononyms this will also indicate equally well the national paronym; but with English and German polyonyms (p. 118) the usual transposition of the adjective and substantive renders the recognition less easy.[1]

(*b*) Abbreviations should be formed regularly, and vowels excluded excepting when the initial letter is such, or when their absence might occasion ambiguity.

(*c*) In the explanation of a figure, abbreviations should be set in alphabetic order. So natural, reasonable, and just is this rule that its disregard can only be attributed to the selfish assumption upon the part of a writer that the time its observance would have cost him is of more value to the world than the time its non-observance costs all of his readers together, not to mention the ill effects of righteous indignation.

Importance of Moderation. — As with biologic generalizations, there are few philologic rules without exceptions. Yet the reformer, especially if young and enthusiastic, either ignorant of history or undismayed thereby, "too often imagines that a principle, if right, cannot be carried too far" (Barclay). In this connection may be appropriately quoted the verse from Horace: —

Est modus in rebus; sunt certi denique fines,
Ultra citraque nequit consistere rectum.

Suggestions to American Anatomists. — Circumstances have precluded the possibility of submitting either the manuscript or the proofs of this lecture to other members of the American committees. Hence their responsibility for its contents must be limited strictly by their official recommendation of certain terms or principles and by the usages embodied in their individual publications. I hope they will join in whatever discussion of the general subject[2] may be aroused by this article freely

[1] From my point of view this constitutes an argument for the conversion of certain polyonyms into mononyms. For example, if the dionym *commissura anterior* be retained, the Latin and French abbreviation would be *c. a.*, the English *a. c.*, and the German *v. c.* But of the mononym, *praecommissura*, *prc.* would probably serve in each case.

[2] The next volume of Merkel's "Ergebnisse" will contain an article upon the subject by Prof. Thomas Dwight.

and without apprehension that opposition to my views will affect my personal or official relations. All I ask of them is the clear recognition of all the conditions.

Perhaps my own view of what the conditions really are may be most conveniently introduced by a commentary upon a paragraph in the address of the president of the Association of American Anatomists a year ago. Professor Dwight said ('95):

> German anatomists have recently adopted a report prepared by some of their number working in company with representatives of other European countries. It is for us to consider whether this one can be looked upon as accepted and whether it is acceptable; whether we can join hands with our foreign colleagues, or whether we can devise an American nomenclature which shall be so much better that we can disregard the inconvenience of a distinct standard. We have had for years a committee on anatomical nomenclature, with Professor Wilder for secretary, who has given so large a part of his busy life to this matter. We may expect an important contribution to the matter in the report of this committee.

Dr. Dwight's address was devoted mainly to what he justly characterized as "a social question of the first importance, far transcending purely scientific discussion, *viz.*, the methods of obtaining and utilizing anatomical material." Nomenclature was considered briefly and almost incidentally. The following commentaries are designed partly to reënforce some of his remarks, and partly to avert possible misapprehension as to both what he said and what he felt obliged to omit.

In the first place, as a member of the committee on nomenclature of the Association of American Anatomists since 1889, Dr. Dwight recognizes with especial clearness that the subject can no longer be ignored. Now that a score of European anatomists have given more or less attention to it during six years, and have expended upon it about $2500, no individual or association can hereafter treat it as insignificant.

Secondly, the approximate completeness of the German list of the visible parts of the entire body renders it a substantial basis for discussion and a starting point for further progress.

The two conditions just named will, as doubtless anticipated by Dr. Dwight, lead anatomic writers and teachers to pay more

heed to their terminology, and to maintain at least a temporary consistency, that is, within the limits of a single lecture, article, or treatise.

Yet our gratification at the tardy German admission of the need of terminologic improvement, and our recognition of the usefulness of the list compiled with such learning and industry and at such expense should not lead us to overlook (*a*) the limitations of the German report in both intent and performance; (*b*) the delay in its adoption by other nations; (*c*) the qualifications of Americans for independent judgment.

The "B. N. A.," that is, the *Nomina Anatomica* adopted by the Anatomische Gesellschaft at Basel in 1895, is regarded by the Germans themselves as provisional and subject to modification. As stated officially (*Anatomischer Anzeiger*, Ergänzungsheft, X, 161) and by Professor His, there was appointed a standing committee of revision, which is to report upon proposed changes and new terms at intervals of three years.[1]

Although France and Great Britain were represented upon the general committee, no members from those countries were present at the signing of the report and of the declaration against the efforts of the American committees, April 19, 1895, (*Anatomischer Anzeiger*, Ergänzungsheft, X, 162). Furthermore, as frankly stated by Professor His ('95, 6–8), some of the French correspondents preferred a different method of procedure, and the English commission had not reported at all. The improbability of universal and unqualified assent upon the part of British anatomists is indicated by the following remarks of a Glasgow professor (Cleland and Mackay, '96, 3):

With regard to the naming of individual structures it may be noted that more than one attempt has been made to impose uniform-

[1] So far as appears in the official record (*Anatomischer Anzeiger*, XII, Ergänzungsheft, 1896), no reference to nomenclature was made at the last meeting of the Anatomische Gesellschaft. Curiously enough, however, the title of a paper (pp. 153, 154) by Bardeleben, who signed the antimononym declaration of the "Nomenclatur Commission" (p. 145), is "Ueber das Praefrontale und Postfrontale des Menschen." I am not disposed to cite these two words as adjectival locatives and as precedents for *postcava*, etc. (p. 150); but they are excellent mononymic adjectives used as substantives (p. 138), and they do not occur in the official list adopted by the committee of which Bardeleben was a member.

ity of nomenclature by the arbitrary authority of an individual or committee.[1] It may be doubted if any such attempt can possibly be successful. The *Nomina Anatomica* of His ('95a) is most important for consultation; but the adoption of its recommendations in this country (Great Britain) would, in a large number of instances, involve the abandonment of good names in general use for others whose advantages are not obvious.

Through its secretary the German committee declared (Krause, '91) that it intended to be "conservative in its action." Now, *conservatism* is notoriously difficult to define, and in respect to nomenclature its degrees may equal in number those who have opinions upon the subject. But, while the abolition of the vast majority of time-honored terms has not been even hinted at in this country, I believe many anatomists here and also in England have recognized earlier and more fully than most of the Germans the existence of two conditions (p. 152, F) that are essentially modern, *viz.*, (*a*) the enormous expansion of anatomic and physiologic knowledge; (*b*) its general diffusion among the people.[2]

Indeed, notwithstanding the declaration of conservatism above mentioned, it is not easy for me to conceive that all the members of the Anatomische Gesellschaft really anticipate the retention of, *e.g.*, "manubrium sterni," "corpus sterni," and "processus xiphoideus" for *praesternum*, *mesosternum*, and

[1] No such attempt is known to me. The very notion savors of ecclesiasticism rather than of science. At the most, individuals have set certain fashions, more or less commendable and permanent, while committees have made recommendations which even their own members may disregard when their information is increased or their views are modified.

[2] For nearly ten years, at Cornell University, the members of the general classes in physiology, candidates for first degree in Arts and Sciences, and numbering from 150 to 180 in each year, have each individually examined, drawn, and dissected the brain of a sheep. At the recent meeting of the American Society of Naturalists, I outlined ('96) a plan for the commencement of practical studies of the brain in primary schools; this in pursuance of the conviction expressed seven years ago: —

"Aside from prejudice and lack of practical direction as to removing, preserving, and examining the organ, there is but one valid reason why every child of ten years should not have an accurate and somewhat extended personal acquaintance with the gross anatomy of the mammalian brain; that obstacle is the enormous and unmanageable accumulation of objectionable names under which the parts are literally buried. W. & G. ('89), § 82.

xiphisternum, respectively; of "squama occipitalis" for (*os*) *supraoccipitale;* of "arcus zygomaticus" for *zygoma;* of "latissimus dorsi," "biceps brachii," and "triceps brachii" for *latissimus*, *biceps*, and *triceps*, respectively; of "processus vermiformis" for *appendix;* of "substantia corticalis" for *cortex;* of "vena cava superior" and "vena cava inferior," "radix anterior" and "radix posterior," for terms not dependent for appropriateness upon the erect attitude of the human body.

In the declaration of the Anatomische Gesellschaft and in the warning of its oldest member it is intimated that between the American and German committees there already exists a terminologic crevice, which further advance upon our part is likely to convert into an "impassable gulf." Taken by themselves, or in connection with the passages just referred to, it seems to me that Dr. Dwight's closing words convey a similar gloomy impression, and that they present alternatives too widely divergent.

As may be seen from pages 127–145, with the single exception of the German retention of *anterior* and *posterior* (pp. 144, 145), between the German committee and the American committees that had reported prior to the three utterances referred to in the last paragraph, the actual differences were really trivial. Even the list adopted by the American Neurological Association contains no unfamiliar term whatever.[1]

It must be remembered also that only neural terms are here referred to. As well remarked by Pye-Smith ('77, 162) and by His ('95, 155), encephalic nomenclature stands most in need of revision and offers peculiar difficulties. With the other regions of the body the conditions and necessities are far simpler. Hence there is no probability that any action of American committees respecting anatomic nomenclature *as a whole* could eventuate in the establishment of what could be regarded justly as a "separate standard." A stronger phrase for the hypothetic contingency could hardly be employed were the dif-

[1] The allegation of Professor His that my individual "proposals tend to create a language entirely new and for the most part quite strange" has already been met (p. 157). In matters non-scientific a deliberate exaggeration of like extent would probably receive a briefer and less euphemistic characterization.

ferences between the two sets of names comparable with the distinctions between the metric system and the English weights and measures.

The address of Dr. Dwight contained no reference to what has already been accomplished or proposed by American organizations. At that time, of course, the action of the American Neurological Association had not been taken. But the Association of American Anatomists and the American Association for the Advancement of Science, at various periods between 1889 and 1892, had adopted unanimously the recommendations of their three committees corresponding with the first five sections of the report of the Neurological Association.

Although the specific terms included in these recommendations are few, they exemplify all the commendable features of the German report. Indeed, I fail to discover in the latter any general statement, principle, rule, or suggestion that had not already been set forth with at least equal accuracy, clearness, and force in the writings of British and American anatomists prior to 1895.

Notwithstanding the small number of individual terms included in the American reports, the dates of appointment of the committees, 1885, 1889, 1891, the representative nature of the terms, and the comprehensiveness of the general recommendations all justify deliberate and independent action upon the part of anatomists in this country. Hence it is gratifying to see Dr. Dwight's indication of our duty in this regard. He evidently advocates neither heedlessness nor a servility that might merit the application of the following caustic comment in an English review of an American work:

Our authors are merely following the lead of a certain eminent German anatomist, it being a fashion with American scientific writers (except a few who prefer a sort of scientific Volapük [1]) to follow pretty blindly the German scientific leads in the matter of nomenclature, and this even to the extent of bodily adopting actual German words

[1] Histologic terminology was apparently referred to here; but I imagine that the remark might apply equally to my series of correlated names for one of the encephalic segments and some of its parts, *viz.*, *metencephalon*, *metacoelia*, *metatela*, *metaplexus*, and *metaporus* (see Table III).

into a language which can already find two or three synonyms for almost any word it may be desired to translate. No doubt many English authors are also to blame in this respect, but the fact is none the less to be deplored.[1] *Nature*, Aug. 13, 1896, 341.[2]

It seems to me that in America the present conditions are particularly favorable to deliberate thought and independent conclusion upon the subject of this article. The professors of anatomy in some of the larger medical schools are young and vigorous. Few, if any, are rightly to be reckoned as "old," or at any rate as too old to change their minds and their modes of expression when occasions arise.[3] In view of all the circumstances, the attitude appropriate for American anatomists, desirous to coöperate yet maintaining their independence and self-respect, is indicated in the following lines of *Lucretius*: —

> *Judicio perpende: et si tibi vera videntur,*
> *Dede manus: aut si falsum est, adcingere contra.*

Those anatomists who are either interested already in the improvement of nomenclature, or whose regard for their successors leads them to sacrifice some present time and effort in their behalf, are urged to read upon the subject, to reflect, to confer, and to correspond freely. So intimate is the relation between verbal expression and mental operation that, even when we imagine ourselves above such weakness, criticism of the former too often means disturbance of the latter. Hence, as with other matters involving individual habit and preference, an actual interview may sometimes be less productive of good than a correspondence that eliminates more completely the

[1] The writer of a letter in *The Nation* for Oct. 8, 1896, declares that "there is a reaction setting in in America against extreme Germanization, and that it has not come too soon." For a comparison of the national *Anlage* with the international *proton*, and a citation of Aristotelian precedents for the latter, see p. 158.

[2] The needless use of German heteronyms has been condemned by Schäfer (*Nature*, July 22, 1897, pp. 269, 270) and by the writer (*The Nation*, May 11, 1894, pp. 349–351).

[3] The following incident encourages the belief that such changes of both opinion and custom may occur at any age. While preparing the new edition of his Anatomy ('89) Leidy preferred *central lobe* or *island of Reil;* but later, at the age of sixty-six, as chairman of the committee on nomenclature of the Association of American Anatomists, he signed the report recommending *insula*.

personal element, and affords opportunity for reflection and for consultation with disinterested experts.[1]

Those who may entertain[2] a not unnatural impatience at the apparently slow progress made in this country, and who may even feel mortified when comparing the two score terms adopted by the American Neurological Association with the forty-five hundred recommended by the Anatomische Gesellschaft, may well consider:

First, the improbability that any competent American anatomist could have been diverted from his regular duties long enough to accomplish what was so effectively done by the secretary of the Anatomische Gesellschaft.

Secondly, the enormous advantage afforded by the complete list adopted by the Gesellschaft. Many dead or dying terms have been disposed of, and the "decks have been cleared" for more efficient action.

Thirdly, whatever precipitation, vacillation, and error may be condoned in individuals whom volition or circumstances may lead to assume untenable positions, organizations legislating in the interest of posterity should advance so slowly as to risk neither recession nor even deflection. The Germans themselves regard their comprehensive list, as a whole, as provisional. The American selections (p. 131) constitute, we may believe, an immortal forty.

Were neural terms to be now devised *de novo*, the hippocamp would certainly receive some less fantastic designation, and the great cerebral commissure would be much more likely to be called *trabs* (a beam) than *corpus callosum*. But both *callosum* and *hippocampus* are embalmed, as it were, in several other names, and they are not sufficiently objectionable to warrant their revolutionary annihilation. The best we can do is to

[1] Nearly all my letters and "slips" from anatomists and linguists in this and other countries have been preserved. Always instructive and often encouraging, the restraining and even destructive quality of some might have been endured with less equanimity at a personal conference.

[2] That such sentiment, if entertained, has not been communicated to me either directly or indirectly constitutes one of the many evidences of the tolerant and helpful spirit that has animated American anatomists in dealing with the confessedly perilous question as to how independent thinkers may best communicate with their fellows.

effect a tolerable compromise between the imperfect conditions that we have inherited and the ideal conditions that we should like to transmit to our successors.

The anatomists of to-day have an opportunity of providing for the future while cherishing the past; of benefiting posterity without neglecting ancestors; of lightening the burdens of generations to come, while recognizing the value of what was done by the anatomical fathers; of erecting a terminologic monument in which the best of what has been is cemented by their own labors.

SEVENTH LECTURE.

A CLASSIFICATION OF THE NORTH AMERICAN TAXACEAE AND CONIFERAE ON THE BASIS OF THE STEM STRUCTURE.

D. P. PENHALLOW.

HERETOFORE botanists have been so accustomed to rely wholly upon characters derived from the external parts of woody plants as a basis of classification that, with few exceptions, it appears to have escaped serious consideration that those external characters which permit us to differentiate families, genera, and species must also be represented by corresponding variations in the internal structure, and, that these, also, may constitute important and reliable data as a basis of classification.

It is now forty-six years since Göppert, in his well-known work,[1] endeavored to establish the relations of certain fossil coniferae to existing species. In the prosecution of this work a number of living species from Europe and America were studied critically with respect to the details of structure as represented in the woody parts of the stem. Numerous figures illustrating the minute internal anatomy accompany the diagnoses of species. So accurate are they that it is possible to determine species from them with as much facility and accuracy as if freshly drawn. The characters are, in fact, precisely those which recent investigations have shown to be of generic and specific value. Although at that time no special attempt was made to formulate a classification on this basis, yet the results detailed were destined to have such an important bearing

[1] Foss. Conif., Leiden, 1850.

upon the question now under consideration that we may well be justified in regarding this notable work as marking the real beginning of a new feature in systematic botany.

During the next thirty years little real interest appears to have centred in this question, although within that period there were issued a number of papers upon subjects having a more or less direct bearing upon it, and the necessity for some more critical method of distinguishing woods under all conditions incidental to their economic application was made evident by the treatise issued by H. Nördlinger for the use of forestry students.[1]

Fully twenty years ago De Bary, in summarizing the results already reached by Göppert, Hartig, Nördlinger, and others,[2] gave a clear exposition of the general basis upon which such a classification might be constructed.

It was not until 1880, however, that special attention appears to have been directed to the desirability of such a line of investigation being taken up seriously. In that year the Vienna Academy proposed, as a subject for the Baumgärtner prize of one thousand florins, "The microscopical investigation of the wood of living and fossil plants," the special object of the investigation being to ascertain characters whereby it would be possible to determine the genus and species with certainty from microscopical sections. Since then the literature of the subject has enlarged somewhat, although the contributors have in almost all cases confined their attention to the investigation of special problems, rather than dealt with the subject as a whole. Although the majority of these do not require citation at the present time, one or two call for more special notice.

An extended examination of the anatomical characters of the stems of dicotyledons in general led Solereder,[3] in 1886, to the conclusion that the characters to be met with are sufficiently constant to admit of distinguishing families, tribes, genera, and species. This is the most important generalization reached up to the present time, and constitutes important evidence in support of similar results more recently obtained.

[1] Die technischen Eigenschaften der Hölzer, Stuttgart, 1860.

[2] Comp. Anat. Phan. and Ferns. [3] *Bot. Zeit.*, XLIV, 506 (1886).

The first serious attempt to construct a system of classification based upon the anatomical characters of the wood of which I have been able to gain information appears to be that of N. J. C. Müller, published in 1888.[1] In this work sixty-five species are illustrated by means of photomicrographs, and the text details the characters of the wood structure as displayed in the three planes of section commonly employed. The figures accompanying the text are very poor and often misleading, while the efficiency of the work is greatly impaired by the fact that attention is not concentrated upon any one group — a few representatives from a rather large number of families being chosen as subjects of investigation.

From the history of the subject as thus briefly outlined it is clear that for some time past botanists have been aware that sooner or later the anatomical characters of the stem must claim recognition as important factors in taxonomy. The need of such a system of classification as now proposed has been apparent not only in the demands arising from an extensive and varied economic application of numerous kinds of woods, but in the requirements of the palaeobotanist who seeks for some more exact means of defining species and of establishing the relations of fossil woods to those now living, than is to be found in a merely general knowledge of structure. When it is recalled that fossil woods are commonly represented by the more durable parts only — a structure from which many of the anatomical details may have been eliminated by the operation of decay or the subsequent alterations attendant upon petrifaction — in consequence of which it becomes of the highest importance that the taxonomic value of such characters as are yet recognizable should be capable of exact estimation, and that wood applied to economic purposes often requires to be recognized under conditions which render the ordinary means of distinction worthless, it is clear that any system of classification which will admit of a precise limitation of genera and species under all conditions, must possess a high degree of value.

With respect to the application of such a classification to living species, the view has been entertained that if species

[1] Atlas der Holzstructur und erläuternder Text.

can be defined at all it will be possible to recognize them under all conditions of growth and economic application. How far such a view may be justified will become apparent upon a careful examination of the generic and specific diagnoses.[1]

With respect to fossil plants, experience shows that the conditions of preservation are extremely varied, so that while a lignite from any given formation may have its structure perfectly preserved, another lignite from a much more recent deposit may show but few of those structural features upon which distinction of species may be supposed to rest.

In accordance with these considerations, it was originally held that any such classification, to be most efficient for all purposes thus indicated, must permit conclusive deductions to be drawn, if possible, from sections of about one centimeter square — such as might be prepared in the ordinary way for microscopic purposes — since this alone would meet the average requirements of material derived from all sources, and more particularly of material representing fossil plants. It is to be observed, however, that such limitations at once impose difficulties which, joined to those due to the fact that the wood alone furnishes the necessary data, might tend to render the classification of inferior value in actual practice. The aim has been, therefore, to select, if possible, those distinguishing characters which may be found in the structure of the woody parts of the stem as exposed in the usual planes of section, — transverse, radial, and tangential, — and to obtain conclusive proof as to their efficiency or inefficiency for the purpose stated. The results so far reached seem to justify the conclusion that for genera the characters are well defined and admit of the recognition of such groups without any question; while for most species they present no greater difficulties than are to be met with under the methods now in vogue.

With these thoughts in mind, attention was directed in the first instance toward the accumulation of authentic material — a work of slow progress, now extended over a period of sixteen years and, with respect to some of the angiosperms, not yet

[1] For a full account of generic characters see Trans. R. Soc. Can., Ser. 2, II, iv, 33.

completed. Within recent date, however, all the various species and varieties of the Taxaceae and Coniferae north of the Mexican boundary have been brought together. This fact, joined to the preëminent position occupied by these plants with respect to their economic importance and palaeontological relations, led to their being regarded as subjects best suited to immediate investigation. The present results, therefore, which deal with the gymnosperms only, may be regarded as the first of a series of similar investigations on the classification of the North American woods as a whole.

Incidentally to the present work, a number of foreign species have been studied, but it has been thought advisable to defer their consideration until opportunity offers for an exhaustive treatment of exotic species.

The whole number of species and varieties included in our present studies is eighty-nine, representing fourteen genera.

The investigations, the results of which are now given, had their origin in 1880. They possess no claim to originality beyond the methods of working out the details, but the results now reached amply confirm the conclusions of Solereder, as already referred to, with respect to the stability of family, generic and specific characters, and, although more extended confirmation is needed before a final statement can be made, it seems possible that varieties may also be recognizable.

The history of the Coniferae abundantly shows that great difficulty has always been experienced, not only in defining the specific limitations, but in establishing the relations between the various genera. Of this there are several notable examples.

Of the closely related representatives of the genus Picea occurring in eastern America, Link distinguished three species, which he designated as P. alba, P. nigra, and P. rubra. Later, botanists on this side of the Atlantic very generally refused to recognize the validity of the latter, which was held to be only a form of P. nigra, and this has been the ruling practice, with one or two exceptions, up to the present time. In 1879, however, Englemann admitted *rubra* as a variety of *nigra*,[1] and this was subsequently admitted as valid by some of our leading author-

[1] Bot. Works, 351; *Gard. Chron.*, N.S., XI, March 15, 1879.

ities.[1] In 1887 the late Dr. George Lawson strongly advocated the validity of Link's species,[2] and this has now found support on the part of Dr. Britton.[3] From this it is apparent that great difficulty has been experienced in defining the specific limitations in these cases, and it has been felt that evidence derived from the internal structure of the wood might serve to determine the balance of evidence in one direction or the other, and thus settle definitely this long-standing controversy. Recent critical studies of these plants serve to show beyond all question that Picea rubra must henceforth be recognized as a distinct species.

The limitations of Chamaecyparis and Cupressus, as also the separation of these two groups from the closely allied Thuya, have formed the basis of a long-continued discussion. The difficulties met with are well indicated in the recent observation of Dr. Masters when he says: "If the two genera (Thuya and Cupressus) had not been so long established and so generally adopted, it might have been well to have included them in one genus, together with Libocedrus, as in all probability all of these have been derived from a common stock. The confusion this would entail in practice would, however, be so great as to outweigh any advantages that would accrue from such an arrangement, theoretically preferable though it might be."[4] As will shortly appear, there are strong reasons on anatomical grounds in support of the contention thus advanced by Dr. Masters for the union of Thuya and Cupressus. In the latter genus we also find that it must now include the former genus, Chamaecyparis, while there is likewise a further question as to whether Cupressus guadalupensis and C. macrocarpa are distinct species, as heretofore considered, or only forms of one species, as suggested by Dr. Masters,[5] who has more recently maintained that C. guadalupensis is a distinct variety of C. macrocarpa.[6]

Finally, we may refer to the great want of agreement as to the relations of the Taxaceae and Coniferae. From these

[1] Gray's Manual, 1890, p. 492.

[2] "Remarks on the Distinctive Characters of the Canadian Spruces," Can. Rec. Sc., VII, 162, 1896. [3] Flora of the Northern States and Canada, 1896, p. 55.

[4] *Journal Linn. Soc.*, XXXI, 313.

[5] *Garden and Forest*, VII, 298. [6] *Journal Linn. Soc.*, XXXI, 343.

examples it is clear that satisfactory conclusions can scarcely be drawn from data which are so widely variable in the same species or group under different conditions or at different periods of their growth, and it would seem that evidence from other sources than the external parts of the plant must be obtained before any stable relations can be established. Under these circumstances, it is scarcely to be doubted that data derived from the internal structure of the wood will go far toward satisfying the requirements of the case, and we are led to the belief that such data must form an essential element in any future discussion of the systematic relations of plants.

The data for a differentiation of the Taxaceae and Coniferae are to be found in the occurrence of resin passages, of isolated resin cells, and of medullary rays containing resin passages, as also in the presence or absence of tracheids with spiral markings.

The Coniferae as a whole are distinguished by their more or less, often strongly resinous wood. This is found in some cases to be due to the presence of numerous large channels, — the resin passages, — which traverse the stem longitudinally for great distances, and such structures are always characteristic of Pseudotsuga, Larix, Picea, and Pinus, more rarely appearing in an imperfectly organized form in Sequoia and Abies. On the other hand, the resinous matter is found to have its origin in isolated resin cells, which are variously distributed either through the entire body of the growth ring or localized along the outer face of the summer wood. In either case their presence may be at once determined by the peculiarly dark and resinous color of the contents, or by the structure of the terminal walls wherever exposed in transverse section. The walls then show a coarsely pitted structure similar to that of a poorly formed sieve plate. The general law of distribution shows that in those woods which have well defined resin passages the resin cells are wanting. Similarly, those woods which have an abundance of resin cells show an absence of resin passages — the one replaces the other. Exceptions to this law naturally occur. Thus in Pseudotsuga and Larix, genera which are distinguished by their prominent resin passages, there are also well-defined

resin cells. So also in Sequoia and Abies, genera conspicuous for their resin cells, resin passages sometimes occur.

Our investigations show that in all genera having resin passages in the wood there are also resin passages traversing the stem in a radial direction and embraced in certain of the medullary rays which have their general form and structure correspondingly altered. Under such circumstances the rays become, as a rule, much higher and always much broader than the ordinary rays. The modification, as exhibited in a tangential section, is such that while the terminals above and below are acute or linear, the central tract is broadened out more or less abruptly, and then consists of one large resin passage and usually also of much reduced parenchymatous cells lying immediately external to the epithelial structure, thus forming the outer limits of the tract. Such rays, which from their form may be designated as fusiform, in order to readily distinguish them from those of the ordinary linear and uniseriate type, are always found in association with resin passages which traverse the stem longitudinally. So intimate is this relation that the presence of one may always be inferred from the other. All North American species of Taxaceae, without exception, show a complete absence of all three of the elements so far considered, — resin cells, resin passages, and fusiform rays. It thus becomes possible, on these grounds alone, to definitely separate this family from all the Coniferae. Among the latter the genus Pseudotsuga stands out prominently as an almost wholly unique instance of a case approaching the Taxaceae in one of its most salient features. In all of the North American Taxaceae, without exception, the tracheids are characterized by the presence of a double series of spiral bands. So distinctive are these structural features that, with one exception, they invariably point to a member of this family. In the genus Pseudotsuga similar spirals are to be met with as a constant element of structure, with this difference, however, that while in the Taxaceae the spirals are a constant element of all the tracheids, in Pseudotsuga they are often entirely absent from the summer wood. They are, nevertheless, always to be met with in the spring wood. Any confusion which might otherwise

arise through the presence of such spirals is at once removed by the fact that, whereas in Taxaceae there are no resin passages or fusiform rays, both of these structures are characteristic of Pseudotsuga. Occasionally other conifers manifest a tendency to the formation of spirals. Thus in Larix americana the outer tracheids of the summer wood sometimes develop very distinct spirals; also in some of the hard pines — notably P. taeda — there is a decided tendency in the same direction. But in none of these cases is the development carried so far as to involve confusion with respect to the law already stated. On the basis of these considerations it becomes obvious that, on anatomical grounds, there is good reason for regarding the Taxaceae and Coniferae as distinct families, a conclusion which serves to materially strengthen similar deductions already derived from general morphological considerations.[1]

The Taxaceae embraces only two genera within the limits of North America north of the Mexican boundary. These are Taxus and Torreya, and between them the principal differential feature is to be found in the shape and size of the ray cells, as exposed in tangential section, and thus to some extent also the width of the ray. Thus in Taxus the cells are oblong and usually very narrow, and investigation confirms the belief that there is no essential deviation from this rule, since the most marked alteration of form occurs in those rays which become more or less two-seriate when the cells are sometimes rather shorter and broader, and thus assume a more or less oval form. In Torreya, on the other hand, the ray cells are always much broader and larger and distinctly oval, more rarely oblong. Supplementary differentiations also appear in the compactness of the tracheid spirals and in the general character of the transverse section. If the compact spirals of Taxus canadensis are compared with the somewhat distant spirals of Torreya californica the distinction between these two genera is at once apparent. Similar differences exist in a more or less pronounced degree between other species of these genera, and they become very obvious in a comparison of Taxus canadensis with Torreya

[1] Geological Survey of California, "Botany," II, 109.
Journal Linn. Soc., XXX, 1.

taxifolia. A third and much less reliable, although valuable, supplementary character is to be met with in the general aspect of the wood as exposed in transverse section. In the genus Taxus the tracheids are chiefly small, thick-walled, variable in size, and with more or less conspicuously rounded lumens, the structure as a whole being rather compact. These characteristics apply with particular force to T. canadensis and T. brevifolia, but are less applicable to T. floridana, since the structure in this species shows a distinct approach to the characteristics of the genus Torreya.

In Torreya the tracheids are relatively large, the walls rather thin, the lumens are, as a rule, more distinctly squarish, while the structure, as a whole, is distinguishable by its rather open texture. While such differences may very correctly be associated with generic distinctions, it must be recalled that the aspect of structure in transverse section varies somewhat widely under different conditions of growth and even in different parts of the same tree, and these variations are of such a nature that it would be quite possible for the wood in a branch of Torreya to present much the same aspect as wood taken from a stem of Taxus. With these considerations in mind, it becomes possible to construct a differential key for these two genera.

The Taxaceae and Coniferae possess a number of structural features in common. These are to be found first in the transverse section, in the usually regularly radial disposition of the tracheids. In the radial section the radial walls of the tracheids of both the spring and summer wood, are marked by the presence of conspicuous bordered pits. In the Taxaceae these structures are relatively small and always in one row, generally occupying the full width of the narrow tracheids. In the Coniferae, on the other hand, they are — with the exception of Juniperus — usually large and oval, or round, and not infrequently two or three seriate. In both families bordered pits occur on the tangential walls of the summer wood, and in a very few cases on the tangential walls of the spring wood of certain Coniferae.

Apart from the details already considered as differentiating these two families, there are few anatomical features which

belong distinctively to the Coniferae, and they are to be regarded as of subordinate value. Thus in tranverse section the tracheids — except in Juniperus — are, as a rule, much larger, and there is often a more marked and abrupt contrast between the spring and summer woods. In the radial section the Coniferae commonly show Sanio's bands, which are wholly wanting in the Taxaceae, so far as it is possible to determine from our present investigations.

Anatomical considerations show that the sequence of genera and also the limitations of those groups, as defined on the basis of general morphology, may require some readjustment. It will therefore be desirable to consider somewhat in detail the various points of affinity which justify the arrangement imbodied in the present treatise.

The four genera, Libocedrus, Cupressus, Thuya, and Juniperus, fall into a natural group, of which the common characteristics are the presence of more or less numerous resin cells, the chiefly simple pits on the lateral walls of the ray cells, the thin or sparingly pitted terminal walls of the ray cells, and the absence of resin passages. A more critical examination of the distribution of the resin cells shows that Libocedrus and Juniperus approach one another somewhat closely in the fact that these elements are disposed in tangential bands, while in both Thuya and Cupressus they are scattering and often appear only in somewhat distant growth rings. The affinity between the first two genera is also greatly strengthened by the great similarity of the terminal walls of the ray cells. There is an important point of divergence, however, in the fact that while in Libocedrus the pits on the lateral walls of the ray cells are simple, in Juniperus they are often more or less conspicuously bordered, a feature which tends strongly to give to this latter genus a decided affinity with Taxodium and Sequoia. The separation of these genera from Thuya and Cupressus thus rests upon well-defined differences in the distribution of the resin cells and the structure of the terminal walls of the ray cells. On the other hand, while Libocedrus approaches them through the character of the pits on the lateral walls of the ray cells, by the same character Juniperus is separable from both

of these genera and finds its affinity with Sequoia and Taxodium. A critical comparison of the remaining generic characters will permit of more exact deductions as to the precise relations in which these genera stand to one another.

Libocedrus.

Transverse. Summer wood, thin, rather dense; the growth rings usually showing a median layer of more dense structure.

Radial. The terminal walls of the ray cells straight or somewhat curved, entire, locally thickened, or even coarsely pitted; the pits on the lateral walls of the ray cells small and simple. Pits on the tangential walls of the summer tracheids very large and numerous.

Juniperus.

Transverse. Summer wood thin but very dense.

Radial. Terminal walls of the ray cells thin and entire, more rarely somewhat pitted; the pits on the lateral walls of the ray cells often with a more or less obvious border. Pits on the tangential walls of the summer tracheids chiefly small and not very numerous.

Thuya.

Transverse. Summer wood thin, the structure rather dense.

Radial. The terminal walls of the ray cells thin and not pitted or locally thickened, usually much curved. Pits on the tangential walls of the summer tracheids small to medium.

Tangential. Ordinary rays narrow, the cells oblong, often very narrow, more rarely oval.

Cupressus.

Transverse. Summer wood very thin, often barely distinguishable; the structure open throughout.

Radial. Terminal walls of the ray cells commonly curved, thin and entire, or often locally thickened. Pits on the tangential walls of the summer tracheids medium to large.

Tangential. Ray cells chiefly broad, oval, or even transversely oval, the rays often more or less two-seriate.

The two genera Thuya and Cupressus are very closely connected, and for a long time morphologists have been unable to agree as to their precise limitations. The Thuya occidentalis of Linnaeus and T. gigantea of Nuttall appear to have been referred to this genus without exception. Cupressus thyoides of Linnaeus was referred by Spach to Chamaecyparis sphaeroidea, by Sprengel to Thuya sphaeroidea, and by Richard to T. sphaeroidalis, a name which has been adopted by the *Index Kewensis* as authoritative.

Cupressus nutkaensis of Hooker, or C. nootkatensis of Lambert, was also referred to the same genus by Trautvetter under the species C. americana. By Carrière it was referred to the genus Thuyopsis, and at different times to T. borealis and T. cupressoides. Both Spach and Walpers referred it to the genus Chamaecyparis, and Fischer also recognized the same genus, but applied the specific name of C. excelsa. The most recent ruling, as embodied in the *Index Kewensis*, indicates that Lambert's name of Cupressus nootkatensis is to be regarded as the authoritative one.

Cupressus embraces five species which have been invariably referred to it, C. macrocarpa, C. Goveniana, C. Macnabiana, C. guadalupensis, and C. arizonica. Cupressus Lawsoniana of Murray has been referred to the same genus by both Gordon and Kellogg, but it has been assigned to Chamaecyparis by Parlatore, Carrière, and Torrey. By the *Index Kewensis* Murray's name of Cupressus Lawsoniana is regarded as the one which holds the greatest claim to recognition. It thus appears that, although recent writers, such as Sargent, have recognized Chamaecyparis as a distinct genus, the tendency has been to divide it up among Thuya and Cupressus. It thus becomes obvious that evidence derived from anatomical data which may tend to throw its weight in favor of one or the other of these views will be of special value.

An examination of the characters already detailed for the genera under consideration will show that the essential distinction rests upon the shape of the ray cells in tangential section and upon the character of the terminal walls of the ray cells. Thus in Thuya the ray cells are distinctly oblong, often quite

narrow, more rarely oval, while the terminal walls of the ray cells are conspicuously devoid of pits, or local thickenings. In Cupressus, on the other hand, the rays are distinctly broader, the cells are oval, round, or even transversely oval, rarely oblong. The walls are also much thicker, as a rule. The terminal walls of the ray cells are thin and often entire, but they also frequently show very obvious local thickenings. These characters are well defined and, so far as a large amount of material will permit a definite conclusion, constant. These characters, therefore, may safely be taken as marking the limitations of the genera. On these grounds, Chamaecyparis nutkaensis of Spach must be restored to the genus Cupressus under Lambert's name of C. nootkatensis. The genus Chamaecyparis thus disappears altogether, a change which is quite in accord with the tendency at present prevalent among morphologists.

It may also be pointed out in this connection that, although characters derived from the aspect of the transverse section are not of leading importance, yet they may serve to confirm differentiations based on other data. We thus find that in Thuya, as a whole, the tracheids are distinguished by their large size, squarish forms, and thin walls. In Cupressus, on the other hand, they are usually more rounded, somewhat smaller, and generally thicker walled. These differences not only agree with the limitations already assigned to Thuya and Cupressus, but they show that the latter approaches the former through C. nootkatensis and C. Lawsoniana. It would thus appear that, on anatomical grounds, there is a very close relationship between Thuya and Cupressus, and that the limitations of the two are not marked by any strongly defined characters. This becomes more apparent when it is recalled that Cupressus thyoides, on anatomical grounds alone, could safely be referred to Thuya sphaeroidalis, but when we consider the weight of evidence to be derived from the external characters, together with those derived from the internal structure, it becomes clear that this species belongs to Cupressus.

From a paper published since these conclusions were reached, it is interesting to note that Dr. Masters has arrived

at the same results as myself, but from data derived from a study of the external characters.[1]

With respect to the genus Cupressus, as now constituted, it may be pointed out that it is separable into two distinct groups, the first of which may be designated as Chamaecyparis, and the second as Cupressus proper.[2] The distinguishing feature of the first section is to be found in the character of the pits on the tangential walls of the summer tracheids, which are narrowly lenticular and not very large. The second section embraces all the remaining species which have heretofore been recognized under this genus. The distinguishing feature is found in the conspicuously large and broadly lenticular pits on the tangential walls of the summer tracheids.

Taxodium and Sequoia approach one another closely in the fact that the pits on the lateral walls of the ray cells are conspicuously bordered, while the same element also serves as the basis of specific distinction. Thus in Taxodium the pits are round and the orifice is narrowly oblong, the border, therefore, broad; while in Sequoia the pits are distinctly oval or elliptical and the orifice broadly oblong, the border thus becoming much narrower and sometimes even obscure. These differences are very well defined and constant, and admit of no doubt as to the particular genus. Both of these genera approach Juniperus in the presence of prominent resin cells, as well as in the fact that these elements are disposed in tangential bands. To this must also be added the fact, already pointed out, that a further affinity is based upon the occurrence in all three, of bordered pits on the lateral walls of the ray cells and similarity of structure in the terminal walls of the ray cells. The occurrence of occasional resin passages in Sequoia sempervirens and a similar occurrence of imperfectly formed resin passages in Abies nobilis point to the fact that there is a strong point of contact between these two genera.

The relation between Sequoia and Abies, thus indicated, is greatly strengthened in other ways, as in the absence of resin

[1] *Journal Linn. Soc.*, XXI, 312.

[2] Dr. Masters' results again accord with my own in the subdivision of the genus Cupressus, although on anatomical grounds I prefer to reverse the order.

passages and fusiform rays, together with the occurrence of isolated resin cells. Abies, on the other hand, approaches the genus Tsuga not only in a closer general resemblance of the structure, as displayed in transverse section, but in the peculiar distribution of the resin cells on the outer face of the summer wood, a character which is likewise common to Pseudotsuga and Larix. In this last character a certain affinity with Picea is indicated, since in the latter the resin cells are wholly wanting, while in Abies they have so far disappeared as to be very scattering and often rather obscure. Nevertheless, the weight of evidence shows that there is no direct relation with Picea, more especially when to the facts already stated we add those elements to be derived from the structure of the ray. In Sequoia and Taxodium there are no ray tracheids. In Tsuga, on the other hand, the tracheids constitute a very prominent feature in the composition of the medullary rays. In Abies all the North American species, with the single exception of A. balsamea, as long since pointed out by De Bary,[1] are devoid of tracheids, and in this single species these structures are to be found but sparingly. The systematic position of this genus, in relation to Sequoia on the one hand and to Tsuga on the other, is thus a matter of well-defined certainty.

The three genera, Tsuga, Pseudotsuga, and Larix, possess the common characteristic of having their resin cells scattering on the outer face of the summer wood. They are also joined by the presence of ray tracheids. Tsuga, nevertheless, stands apart, and finds alliance with Abies, Sequoia, and others of that group through the absence of resin passages and fusiform rays, elements which are not only prominent in Pseudotsuga and Larix, but also in Picea and Pinus. Pseudotsuga, Larix, and Picea are yet more closely related by reason of the great similarity of the fusiform rays. These structures, within the limits of this group, are generally distinguished by the rather abrupt contraction of the central tract into linear terminals, which often become much prolonged. The cells are thick walled, and the resin passage is chiefly devoid of thyloses, while the epithelium cells are thick walled and form a distinctly undulating

[1] Comparative Anatomy, 1884, p. 490.

outline to the central passage, or space. A separation of these three genera then becomes possible, in the first instance, from the fact that in Picea there is a total absence of resin cells, a fact which serves to give it direct connection with Pinus. Pseudotsuga is the most clearly defined of all genera by reason of its spiral tracheids, a feature which serves to differentiate it not only from Larix, but from all other genera without question. In cases of possible doubt, however, such as might arise through the removal of the spirals by decay, it may be borne in mind that a further differentiation appears in the large size of the resin passages in the fusiform rays of Larix, while in Pseudotsuga they are small and often nearly closed.

The genus Pinus stands by itself as a well-defined group, which it is impossible to confound with any other genus. As already pointed out, it possesses certain characteristics in common with Picea, Larix, and Pseudotsuga, by reason of the presence of resin passages and fusiform rays, as also in the invariable presence of ray tracheids. It is unique, however, not only in the character of the fusiform rays, but in the nature of the pits on the lateral walls of the ray cells and in the structure of the cells themselves. To these features may also be added the fact that the resin passages are large, always with thyloses, and the epithelium cells are thin walled, forming an entire boundary to the central space. Within its own limits, the genus presents certain well-defined differences, which permit of its separation into two subordinate groups, or sub-genera. The first of these divisions is distinguished by the presence of bordered pits on the tangential walls of the summer wood, while the second is distinguished by the entire absence of these elements.

From the relations thus indicated the various genera have been arranged in such sequence as to exhibit as nearly as possible their true genetic affinities, and the order now adopted may be taken as expressing these relations in their principal aspects. I am fully sensible, however, of the many imperfections which must enter into a work of this nature — a work which is announced for the first time and has not yet gained that measure of solidity which can only come from its actual

application to the purposes for which it is intended. It is, therefore, my hope that those who may have occasion to use it will report any serious deficiencies or point out any alterations which may tend to increase its working efficiency.

EIGHTH LECTURE.

THE SELECTION OF PLANT TYPES FOR THE GENERAL BIOLOGY COURSE.

JAMES ELLIS HUMPHREY.

It was Professor Huxley who first gave expression to the fact that the study of animals and plants is "one discipline," and embodied his conviction in a laboratory course in general biology. In the United States such courses have been as widely adopted as in Great Britain, chiefly through the influence of the Johns Hopkins University, whose biological teaching was largely organized by Huxley's disciple and collaborator in the preparation of the first published handbook of such a course, Prof. Newell Martin. The flood of handbooks, more or less closely following this original model, which has appeared in fifteen years bears sufficient testimony to the popularity of the main plan of instruction. It seems to-day an axiomatic proposition that the zoölogist should know something of plant life and that the botanist should not be a stranger to animals. And there can be no doubt that a well-directed study of fundamental types of both kingdoms, relatively early in the course, affords at least one of the best means of preparation for subsequent specialization in either of the departments of pure biology or for the study of medicine, which can be intelligently taught only as applied biology. I believe, then, that the underlying idea of the general biology course is sound. But it must be well carried out to be really serviceable. Undoubtedly, the sympathetic coöperation of a botanist and a zoölogist would lead to the best results; but far better than the independent and uncoördinated work of two persons would be that of a single

broadly trained teacher. It is not supposed that the following discussion contains anything new. It has been suggested by conversations with college teachers of biology, and is offered with the wish to correlate the two aspects of the work of the Marine Biological Laboratory and to make its botanical work an integral part of the whole.

Most chairs of biology in America are now held by zoölogists who have their own ideas about the choice of animal types, but trust to books or follow the example of some teacher in the selection of the forms of plants to be studied. It is equally true that most of the laboratory handbooks in general biology have been written by men who are chiefly zoölogists, and who, in their turn, have been guided more by example than by a wide knowledge of plant forms in the choice of types, however well the chosen types may have been treated. Thus it has happened that certain plants have come to be regarded as classic forms for use in such a course of instruction. And not a few botanists seem to have been more impressed by the weight of precedent than by any consideration of the real representative character of the plants in question. The ease of obtaining suitable material of a given plant may fairly receive some attention in the selection of types, but it is evident that in some cases the long-continued and now confirmed use of badly chosen forms rests on a quite erroneous impression of the difficulty of obtaining suitable ones, or on unwillingness to make a slight effort in obtaining or becoming acquainted with new plants. If this paper shall aid in banishing some untypical "types," and in replacing them by others more useful, one of its purposes will have been realized.

The *purpose*, then, of the so-called general biology course should be twofold. It should aim to give an intelligent conception of biological methods and problems as a part of a liberal education, and it should lay a foundation for future study in pure or applied biology. Incidentally to these chief aims it may be used to convey some knowledge of the structure and relationships of the chief great groups of plants and animals. Its *place* is in the college, *not* in the high school. A parenthesis here concerning high-school work in biology may not

be amiss. The very common attempt of secondary schools to ape the colleges and to anticipate their work is a grave mistake, and nowhere has this tendency been more marked than in biological teaching. It has been due in large measure, doubtless, to the imperfect training of many high-school teachers, whose chief biological stock in trade consists of the notebooks of the general biology course. But it has also been due to a widespread failure to appreciate the fact that the experience which enables one to see well with the compound microscope is readily gained only after one has learned to see with the unaided eye. And the system of cramming and memorizing of our primary schools brings pupils to the secondary schools with atrophied powers of observation, and at an age when the logical powers are still rudimentary. The purpose, then, of natural history work in high schools should be primarily to develop the ability to observe and to reason from observation by the simplest and most familiar means, without the intervention of technical or material difficulties. This training may carry with it a good deal of information concerning the grosser structure and vital activities of plants and animals, as they may be made out by the aid, at most, of a hand lens and of simple experiments. On the plant side it may give a conception of *morphology*, as illustrated in the modifications of foliar organs, for example; of *physiology*, from the functions of roots and leaves; and of the significance of the *life cycle*. It may also illustrate *classification* as based on structure and the value and meaning of distinctive characters. Such a training would send to the colleges students who can observe accurately and think about what they see, prepared to learn the use of means for extending the range of their observations. This I believe to be an important preparation for the general biology course. As a rule, such preliminary training ought to be insisted on, and would render the work of that course much more thorough and profitable.

As a college course, then, following the preparatory training just outlined, what plant types can the general biology course most profitably present? They ought fairly to illustrate plant life and the structure and physiology of the great groups of

the vegetable kingdom, which, for this purpose, may be called the *Algae*, *Fungi*, *Bryophytes*, *Pteridophytes*, and *Spermatophytes*. The representatives here chosen are not suggested with any belief that they are the best possible, but with some view to their availability in Eastern North America and with some confidence that they are much better adapted to the purpose than those used in many such courses and described in various handbooks. In several published schemes the number of plant types presented varies from nine to fifteen, and we may take the mean as giving about the number of forms that can be satisfactorily studied in the botanical half of the course. The great variety of structure among the Algae and Fungi justifies the selection of a third of the dozen types from each of those divisions, leaving the other third to be chosen from among the higher plants.

Since the Algae include the simplest of typical plants and represent the beginnings of the various lines of plant development, they deserve careful study. Their chief features may be illustrated by the following: —

1. An unicellular Alga, like the *Pleurococcus* that often forms green stains on the bark of trees, multiplying only by division, or *Tetraspora*, found in gelatinous colonies in ditches and pools in spring, or the *Haematococcus* (Sphaerella) of rain-pools, with its ciliate motile stage and its brick-red resting cells, may serve to emphasize the simplicity of form and structure of primitive organisms and to illustrate fundamental vital phenomena.

2. *Spirogyra*, or some similar Conjugata, presents a striking case of the beginning of sexuality and of the association of cells in a loose union. Theoretically, a zoösporic form, like *Ulothrix*, would be preferable as showing an equally primitive sexuality with ciliate gametes, the forerunners of the spermatozoids of the higher plants; but the difficulty of obtaining plants that show zoöspores or gametes, and the far greater difficulty of observing the union of the gametes, makes its use impracticable.

3. *Fucus*, the rockweed of our seashores, with its massive structure and apical growth and its well-defined oögamy, pre-

sents a great advance in complexity and the essential features of that general reproductive type which characterizes the great majority of plants. The masking of the chlorophyll by a secondary pigment, peculiar to so many marine Algae, is here well shown. If distance from the seashore or other causes make it too difficult to obtain this plant, it may be replaced by *Vaucheria*, which grows in green mats in brooks and springs. Its oögamic reproduction is as typical as that of Fucus, and it illustrates the structure of the remarkable siphonaceous group of Algae, which presents such complication of external form in tropical seas.

4. *Batrachospermum*, common in flowing currents of fresh water streams, shows the peculiarities of the red Algae in its thallus, built up of branching filaments, and its spore-tufts, each the product of a single sexual union.[1] Here is the basis for all the extraordinary variations of the carposporic type of reproduction which finds its culmination in this group. Equally useful and almost identical in structure is the slippery *Nemalion* which covers many a bold rock that is uncovered at low tide all along our coast, but rarely more abundantly than at Wood's Holl and on the neighboring islands.

Our list of Algae is complete without mention of the old friend of many years and much searching, the stonewort, Chara. It is impossible to see what conditions have determined the survival of this feature of the original biology course for so many years, except its ready accessibility in some regions and the force of habit. Its vegetative structure and its reproduction are characteristic of nothing but the isolated little family to which it belongs. Unique in almost every respect, and highly specialized, these plants illustrate no important feature of vegetable life in so characteristic a form as do many Algae, with the exception of protoplasmic rotation, which is by no means a general phenomenon. They throw no light on the structure or relationships of other plants, and even their own systematic position is doubtful, for they are hardly Algae, on the one hand, or Bryophytes, on the other. It is quite time

[1] For our present purpose it is not necessary to discuss existing differences of opinion as to the physiological necessity for the act of fertilization in some red Algae.

that their use as representative plants and the resulting misconceptions among students were abandoned.

The Fungi most strikingly exemplify the ability manifested by some plants of nearly all the great groups to adapt themselves to saprophytic or parasitic life with loss of their chlorophyll and thus of the independent food-making power which characterizes normal plants.

5. *Saccharomyces*, the baker's yeast, presents a fungus of very simple structure, and illustrates in its manner of life the essential features of saprophytism and the phenomena of fermentation. It is instructive to compare with the yeast some of the Bacteria which produce the decomposition of organic substances, both from a physiological point of view and as examples of the smallest and most simply organized of known plants.

6. *Rhizopus*, which appears abundantly as a black mold on bread, is closely comparable in its sexual reproduction with the conjugate Algae, and presents in simple form one of the characteristic organs of non-sexual reproduction among the Fungi, the sporangium. The siphonaceous structure of its filaments recalls that of Vaucheria. If it be preferred to use a form quite closely comparable in its chief features with Vaucheria, one of the aquatic fungi, *Saprolegnia* or *Achlya*, may be used. They are readily cultivated on dead flies in water from ditches or pools.

7. Another familiar acquaintance of long standing among teachers of biology, which apparently owes its continued use to its ubiquitousness, is the blue mold, Penicillium. But the small size of its conidia and the complicated structure of its conidiophores make it inconvenient and less instructive than other forms; besides which, it practically never develops its sexual fructification. Equally unsatisfactory in the former respect, but far better in the latter, is the common mold of fruit preserves, whose greenish conidial stage (Aspergillus) is followed by the yellow sexual fruits (Eurotium). And much better than either of these is the closely related *Microsphaera* of the lilac or any one of the "powdery mildews." These may be obtained in abundance with a little care, each summer, and are

preserved by pressing the leaves on which they grow or by placing them in alcohol. The large and simply formed conidia are developed in midsummer, while the primitive, readily understood sexual fructifications follow in early autumn. They serve to show the salient features of the Ascomycetous group, comparable in its reproduction with the red Algae, and they illustrate clearly the important phenomena of parasitism, showing the haustoria by which the cells of the host plant are robbed of their contents.

8. *Agaricus*, the mushroom, obtainable at any time in the city markets and readily preserved in alcohol, has a highly specialized fructification, representing the culmination of one of the lines of development in the great non-sexual Basidiomycetous group. The building up of a structure so highly differentiated externally from simple filamentous elements is instructive. If time permits, it is of interest to examine a lichen, at least sufficiently to show it to be composed of a fungus, commonly ascomycetous, and an alga living in intimate and peculiar association.

As we pass to the higher plants, the comparative similarity in the life history of the members of each great group makes a single type do much broader service. The development of the Bryophytes is, in its essentials, so uniform that a single example may serve to illustrate it.

9. *Pellia* or *Pallavicinia*, or a similar thallose liverwort, seems to me, on the whole, best suited to the purpose. From the study of almost any Bryophyte the idea of the alternation of generations may be readily gained, but the comparison of the simple thallus of Pellia with the prothallus of the Fern is instructive; while its relation to the leafy mosses is less important, since these represent a side shoot from the main line of plant development. The simple sporogonium of the Hepatics is also much more typical than the complicated moss capsule. The most familiar Bryophyte type for this use probably owes its selection to its very common occurrence in some localities, but a member of the group less adapted to the purpose could hardly be named than this Marchantia. Its massive thallus is very highly specialized and of a structure peculiar to

a small part of the Hepatics. The stalkless sporogonia are borne on specially developed, erect portions of the thallus, which are found only in this single family. The primitive Bryophyte structure and life history are so masked by the modifications which Marchantia presents that good students distinguish between the fundamental and the accessory features with difficulty. A very capable and generally well-trained student at the Marine Laboratory, while studying Pallavicinia this season (1896), exclaimed, as she comprehended its simple and typical life history, "Why, it is just like a moss." Her previous acquaintance with the Bryophytes had been gained from the study of Marchantia and a moss, and their essential similarity had been quite concealed by the secondary modifications of the former. Such Hepatics as those above recommended may be found in wet, boggy ground and about springs, and many times repay the additional effort required in obtaining them. Both of those mentioned produce their sexual organs in summer and bear the young sporogonia in autumn.

It is impossible to give an adequate idea of the Pteridophytes by means of a single type, but if only one can be used there is no doubt what it should be.

10. *Pteris*, or some other common fern, illustrates in its large green prothallus and its vascular, leafy, sporangium-bearing sporophyte, the life history of all the vascular plants, and represents one of the earliest stages in the line of development which culminates only in the highest seed plants. If time permits, it is very helpful to examine the fertile spikes of a species of *Selaginella*, either one of our own or of such as are to be found in almost any greenhouse where ferns are grown and their prothalli are obtained. Here is seen a simple case of heterospory, that condition which has arisen in each of the principal Pteridophyte groups, and which is permanent in all the seed plants. A very brief study of such a form makes the passage to the Spermatophytes and their relations to the Pteridophytes much more intelligible. The two groups of Spermatophytes show so little in common, apart from the investment of the embryo by protective and nourishing tissues to form a seed, that each should be studied in one illustrative

form. Of the Gymnosperms only the largest and most important group, the Conifers, is represented in our temperate flora.

11. *Larix decidua*, the European larch, is very commonly planted as an ornamental tree, and possesses advantages over most other available species. Its fertile cones mature in the same season in which they appear, and their tissues do not become inconveniently hard for cutting until quite late. Both sorts of cones are produced pretty freely on the lower branches, where they are readily accessible. In structure the cones are as typical as those of the pine or spruce, and in one or more of the respects above mentioned they are better than those.

12. *Fagopyrum*, the cultivated buckwheat, or a large-flowered species of *Polygonum* may perhaps serve as well as anything if it is desired to follow out the angiospermous life history in a single plant. On the other hand, many of the *Liliaceae* show the arrangement of cells in the embryo sac before and up to the time of fertilization with especial clearness, and many other plants are particularly favorable for the study of certain other details. The bean and other *Leguminosae* show the structure of a primitive ovary, but its ovule is peculiar, and the absence of a permanent endosperm in the seed is a disadvantage.

It must be evident that this is not an attempt to furnish a guide to the study of the types proposed. A few of the more salient features illustrated by the forms suggested have been barely mentioned, and may serve as hints, to be taken for what they are worth. But enough has perhaps been said to make clear the writer's conviction that phylogenetic considerations are important in such a course. The general idea of progressive development and increasing complexity ought to be everywhere brought out to give coherence and unity to the work. But this is impossible if the course be a helter-skelter mixture of plant and animal types. It may be urged that the sequence of types in the latter case is never an unconsidered one, but allows an instructive comparison of certain plants with certain animals. Granting this, it is yet difficult to see how any adequate compensation for the sacrifice of conceptions of descent and relationship is possible. Biology without phylogeny may be compared to a cell deprived of its nucleus, not dead, perhaps,

yet robbed of the power of development. Therefore, the importance of a connected study of the types of each kingdom would seem to be self-evident.

But little consideration is necessary to show whether plants or animals should be first studied. Their generally less complicated structure and their much less complicated physiology, so far as general principles are concerned, the greater clearness with which they illustrate such fundamental facts as those of cellular structure, and the fact that they are the primary elaborators of organic substances all mark the plants as best adapted for study by beginners and for the elucidation of the elementary phenomena of living beings.

A half year of such work as has been here outlined, followed by a similar study of animal forms, ought to lay a substantial and most useful foundation for future studies in medicine or in zoölogy or botany.

NINTH LECTURE.

THE RATE OF CELL-DIVISION AND THE FUNCTION OF THE CENTROSOME.

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There are few phenomena that bring us so close to the fundamental problems of organic development as do those which relate to the origin of the egg and the spermatozoön, to the union of these cells in fertilization, and to the early divisions of the fertilized egg-cell. The egg and the spermatozoön represent the manifold qualities of two separate individuals, and by their union a new individuality is established. In the form and arrangement of the cells into which this oösperm divides, we can recognize the rudiments of the adult body often before the cells become too numerous to be counted; indeed, in many animals the early cleavage-cells constitute a free swimming larva of specific form and possessed of definite functional cellular organs, before the constituent cells are seventy in number, and within four or five hours after the egg is fertilized.

When the organism is composed of so few cells, it is obvious that the specific form of the body, — the size and relations of its organs, — is directly dependent upon the size of every component cell in comparison with the others, upon the position which the several cells occupy in the whole aggregation, and upon the number of cells which perform the same function and constitute a particular organ. The cells which compose the body at a later period of development are but the lineal descendants of those which compose the early larva, and the

conclusion follows that the form of the body at any period of development is a resultant of (*a*) the *relative size of the cells* which constitute the several parts, (*b*) the *direction of the cleavage* to which the cells owe their position, and (*c*) the *rate of cleavage* of the various blastomeres, *i.e.*, the intervals of time between successive divisions, by which the number of cells in any part is determined. If we could discover the factors which determine respectively these three component features of development, we should have material for an explanation of the origin of the specific form of the animal body, embryonic or adult.

The problems relating to the rate of cleavage and the size of the resulting cells have received much attention from various investigators, and we will limit ourselves for the present to a consideration of the third factor — *the rate of cleavage*. The effect of the rate of cell-division in determining the form of the embryo is well shown in the early stages, especially in those forms in which the cleavage is "constant and determinate." When the blastomeres in one part divide faster than those in another, important changes take place in the form of the embryo. The "teloblasts" in Clepsine, Rhynchelmis, and Lumbricus, for example, early give rise by their rapid divisions to the germ-bands of the nerve-cords, nephridia, muscles, and other portions of the ventral plate of the trunk, while the divisions of the cells near the apical pole are less rapid, and this region changes more slowly. If the form of the embryo is affected by the differences in the rate of cell-division in certain regions, our problem is to find out the factors which account for these differences. In seeking them, let us first examine the cell-division in the early stages of the embryo, and afterwards those which occur later in the life-cycle.

The "cleavage stages" in certain annelids and mollusks are especially favorable for our purpose, because the behavior of particular cells can be followed with precision, the cells being few and their manner of division constant. In the annelid Amphitrite, up to about the 64-cell stage, the differences in the rate of division among the various blastomeres are comparatively slight, so that all sixty-four cells belong to the same generation

(Fig. 1). In the subsequent cleavages, however, the differences are very pronounced, and the cells may be classed in four categories, according to their peculiarities with reference to the rate of division: (1) cells which divide much more rapidly than any of the others, *e.g.*, those marked *x* and *m* in the diagram, which form respectively the ectoderm and the mesoderm of the trunk; (2) cells which divide more slowly but continuously, *e.g.*, *ec*, which form part of the general ectoderm of the head; (3) cells which cease dividing for a considerable period, but later resume their karyokinetic activity and undergo rapid segmentation, *e.g.*, the entoderm cells, stippled in the diagram; (4) cells which never divide nor show any signs of karyokinetic activity, *e.g.*, those marked *p*, and these soon develop motile cilia and constitute the primary prototroch,—a larval organ of locomotion. In the latter category may be placed also the cells marked *p'*, for three of the four cells derived from the division of each of these also cease dividing, become ciliated, and contribute to the formation of the prototroch.

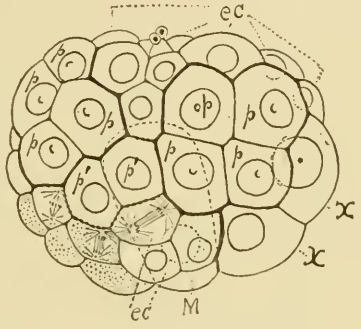

FIG. 1. — Side view of the egg of Amphitrite at about the 64-cell stage. The heavy lines indicate areas of differentiation; *p*, primary prototroch-cells; *p'*, secondary prototroch-cells; *x*, somatic plate; *ec*, general ectoderm; *m*, mesoderm; stippled cells, entoderm.

What are the influences which compel the prototroch cells (*p*) to cease dividing, while the adjacent cells (*x*) divide with extraordinary rapidity? Why do the cells of the general ectoderm (*ec*) divide at an ordinary rate, while karyokinesis in the neighboring entoderm cells is temporarily suspended?

Many more or less plausible suggestions as to the nature of the extrinsic conditions which determine the behavior of cleavage cells have been advanced by students of developmental mechanics, the gist of which is tersely expressed by Driesch: *The prospective significance of a blastomere is a function of its position*, the effects of mutual pressure, of surface tension, of gravity, etc., varying according to the position of the blastomeres in the egg, and according to the position of the egg itself.

That the environment of a cell due to its *position* in the egg does not account for its rate of cleavage in the egg of Amphitrite would appear from the following: (1) adjacent cells may have entirely different rates of cleavage, the one dividing not at all, the other dividing rapidly; (2) cells which occupy exactly corresponding positions in different quadrants of the egg exhibit great diversity in the rate of cleavage; (3) the power of dividing is *suddenly* lost in the cells which form the prototroch — there is not a gradual waning of karyokinetic activity in the successive generations preceding these particular blastomeres; (4) the rate of division in the various cells is the same in whatever position the egg may lie.

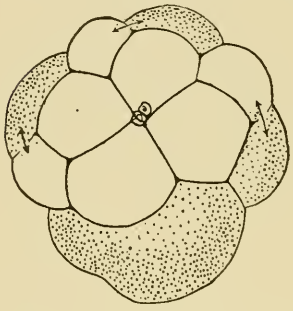

FIG. 2. — Egg of Scolecolepis from above. The four cells at the animal pole undivided; the yolk-laden cells at vegetative pole undergoing division.

Moreover, in related eggs of the same cleavage type, certain blastomeres have a very different environment by virtue of the difference in the absolute and in the relative size of their neighbors, but the rate of cleavage does not vary accordingly. Thus, the cells which form the prototroch in Amphitrite, Clymenella, and Arenicola, respectively, are different in their absolute and in their relative size; yet the cessation of division occurs at exactly the same period of cell development in all three annelids.

Balfour's generalization that the divisions occur more frequently or less frequently according as the cells contain little or much yolk in proportion to the protoplasm has been shown by many observers to be of only limited application. One of the annelids well illustrates the inadequacy of this "law." In the 8-cell stage of Scolecolepis the four lower blastomeres contain all the yolk of the egg and are many times larger than the four upper blastomeres, which are free from yolk; and yet the four yolk-laden cells divide sooner than those which contain only pure protoplasm (Fig. 2).

The same differences in the rate of division that exist in the early cleavage of the ovum obtain in the later stages of the

life-cycle. The cells constituting the Malpighian layer of the epidermis in vertebrates and the apical "budding zone" in certain annelids continue to divide throughout life. Other cells, in which for a long time karyokinetic activity is suspended, may upon occasion undergo rapid division; *e.g.*, the cells which give rise to the temporary ovaries in some of the

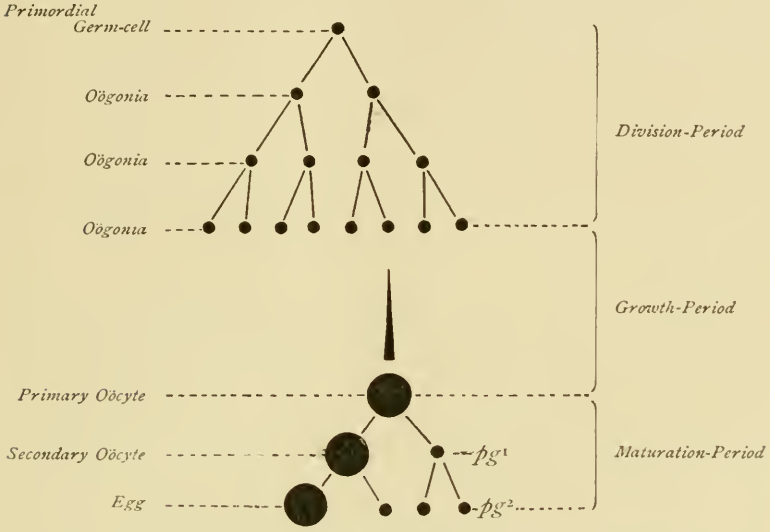

FIG. 3. — Diagram showing the development of the mature egg from the primordial germ-cell (after Boveri).

lower invertebrates and the cells which commence the regeneration of lost tissues. Many cells also, *e.g.*, the neuroblasts, cease dividing permanently.

I wish, however, particularly to call attention to the peculiarities in the rate of cell-division exhibited towards the close of the life-cycle by the cells which give rise to the mature ovum. After a long series of consecutive divisions of the oögonia (Fig. 3), a generation of cells arises in which karyokinesis is, for a time, suspended. These cells are the *un*maturated eggs — the "*primary oöcytes*." The oöcyte, after enjoying a period of rest and growth (which may sometimes be measured in months or even in years), sooner or later divides into a small cell — the first polar globule, and a large cell — the *secondary oöcyte*. The latter also divides to form a small cell —

second polar globule, and a large cell — the mature egg. With this division the life-cycle is completed, the mature egg representing the last generation of cells.

Beginning with the formation of the primary oöcyte, the phenomena of cell-division recall those in the cleavage stages of Amphitrite. In the oöcyte, as in the cleavage-blastomeres, we meet with cells which cease to divide temporarily and with others of a definite generation which, left to themselves, never divide. The peculiarities in the rate of division of the oöcytes are rendered more significant by the fact that in almost all known cases, in both animals and plants, the same phenomena obtain, *viz.*, that not more than two successive divisions of the primary oöcyte take place (unless fertilization occurs to initiate a new cycle of division) before there is a permanent cessation of mitosis.

It is now pertinent to ask, *What are the factors which determine the rate or time of division of the oöcytes, and why does the maturated egg cease dividing until fertilization takes place?* That the behavior of the oöcytes is not a "function of their position" is evident from the enormous differences in the physical surroundings of various eggs at this period. Is there any known structure *within the cell* by whose activity the division may be incited and in whose absence the cell cannot divide? Boveri's theory of the *centrosome*, which has been endorsed by a large number of eminent workers, gives an affirmative answer to this question. According to this theory, the centrosome is necessarily present in mitosis; the attraction sphere, astral rays, and spindle fibers of the mitotic figure arise under its influence. The centrosome is, in fact, the special organ of cell-division, — "the active centre of cell-division in the cell-body."

It is interesting that a large part of the evidence in support of this theory has been drawn from the behavior of the centrosome in the maturated ovum, the cell now under discussion. According to Boveri, this cell is unable to divide because it has lost its centrosome through degeneration. It may resume karyokinetic activity only when a new centrosome is brought in by the entering sperm. "The ripe egg possesses all of the

organs and qualities necessary for division excepting the centrosome, by which division is initiated. The spermatozoön, on the other hand, is provided with a centrosome, but lacks the substance in which this organ of division may exert its activity. Through the union of the two cells in fertilization all the essential organs necessary for division are brought together ; the egg now contains a centrosome which by its own division leads the way in the embryonic development." "It is the centrosome alone that causes the division of the egg." [1]

The behavior of the centrosome in fertilization, as recorded by many recent observers, *may* be interpreted as a substantiation of Boveri's conclusions, for the centrosomes which are demonstrable in the egg during those divisions which result in the formation of the two polar globules totally disappear, and the centrosomes which participate in the first cleavage mitosis arise at any rate *near* the sperm-nucleus, and, moreover, in many instances are actually brought into the egg by the spermatozoön (Boveri, Wilson, Matthews, Hill, Fick, Henking, Kostanecki, and Wierzejski, Rückert, and others). In parthenogenetic eggs, where no spermatozoön enters, the centrosomes ought, according to Boveri's theory, to remain and to organize the machinery for the first cleavage mitosis. Brauer has shown that the parthenogenetic egg of Artemia fulfills the requirements of this theory, for the egg centrosomes actually remain and form the cleavage amphiaster.

These observations furnish ground for the belief that the egg-cells cease dividing, because they lack the active agent in cell-division, — the centrosome. The loss of this organ has been regarded as a "provision to guard against parthenogenesis." Thus, according to this interpretation, the rate of cell-division in the cells of at least one generation is conditioned upon the presence of the centrosome.

Since the essential features of mitotic division are the same throughout the life-cycle, it would seem probable, *a priori*, that the factors which inhibit or incite the mitotic activity of the egg-cells would also determine whether the cells of other generations should or should not divide. Or, to be more

[1] Boveri, Wilson "Cell."

explicit, if the division of the mature egg-cell is inhibited because its centrosome degenerates, and is subsequently resumed because a new centrosome is introduced, it is fair to infer that the division of a blastomere, a tissue-cell, or an *oöcyte* is also conditioned upon the presence of the centrosome. For example, the prototroch-cells in the annelid larva, or the neuroblasts in the vertebrate embryo, cease to divide because the "centrosomes by which division is initiated" have degenerated. Again, the cells by whose rapid division lost tissues are regenerated resume their mitotic activity upon the acquisition of a centrosome.

With this explanation in mind, let us return to a more critical examination of the phenomena of mitosis in the germ-cells at the close of the life-cycle; *viz.*, to the division of the primary and the secondary oöcytes and the mature egg.

It is noticeable, in the first place, that among different species of animals the mitosis is not always suspended in the same generation of cells. Accordingly, the eggs of the various species may be arranged in five classes: first, those in which the primary oöcyte remains with germinal vesicle intact until the sperm enters (for example, Thalassema, Nereis, Fig. 4, *A*); second, those which, if deposited in sea-water, remain with the first maturation amphiaster in the metaphase (for example, the annelid Chaetopterus, Fig. 4, *B*); third, those in which the secondary oöcyte awaits the spermatozoön (for example, the frog, Axolotl, lamprey, Fig. 4, *C*); fourth, those in which the maturated egg, after the formation of both polar globules, awaits the sperm (for example, the sea-urchin, Fig. 4, *D*); and fifth, those (parthenogenetic eggs) which begin the subsequent cycle of divisions without being fertilized.

Let us grant for the moment that the parthenogenetic egg continues to divide because its centrosomes do not degenerate, and that the fertilized egg of the sea-urchin divides because the entering sperm brings in the centrosomes which organize the machinery of mitotic division. It is difficult to apply the same principle to the eggs of the first, second, and third classes, *i.e.*, to those which do not complete the maturation divisions until the spermatozoön enters, for the amphiasters of the matu-

ration divisions do not involve the sperm-centrosomes, but are separate and independent of them. The first maturation amphiaster in certain eggs, *e.g.*, Thalassema, Nereis, and Myzostoma, is formed only after the sperm enters, and yet its centrosomes are not brought in by the sperm nor do they arise near it. In Chaetopterus, on the other hand, a complete amphiaster with centrosomes, centrospheres, astral rays, and spindle fibers is developed and remains for hours in the meta-

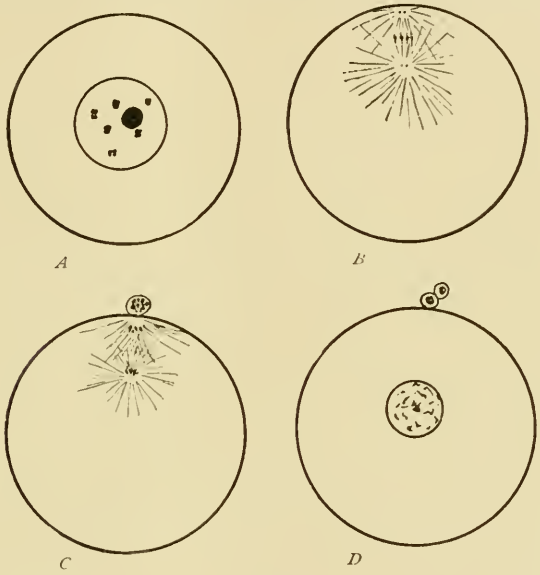

FIG. 4. — Diagram indicating the different stages of maturation attained by the eggs of various animals before the sperm enters. *A*, Nereis, Thalassema; *B*, Chaetopterus and some other marine annelids; *C*, frog, Axolotl, lamprey; *D*, sea-urchin.

phase, if the egg is left unfertilized in sea-water; and the same appears to be true of many other marine annelids. This elaborate machinery of mitotic division is immediately set in motion upon the entrance of the spermatozoön, though the sperm and its centrosomes are in a distant portion of the egg. All the phases of this and the subsequent mitosis are independent of the karyokinetic changes in the vicinity of the sperm.

Since in one form the oöcyte will not divide until the sperm enters the cell, even though the *centrosomes* and the whole

amphiaster *are present*, the suspicion is warranted that in the ripe egg of other forms — the sea-urchin, for example — the mitosis is not inhibited merely on account of the *lack of a centrosome*, nor is it incited merely because a new centrosome is introduced to organize the mitotic figure.

Other observations on fertilization strengthen this supposition. Wheeler has shown in Myzostoma that no centrosomes or asters are developed in connection with the male pronucleus, and that the centrosomes, which are left in the egg after the formation of the polar globules, probably form the poles of the cleavage-spindle. According to Lillie, the sperm-centrosomes in the egg of Unio degenerate, and the centrosomes which participate in the first cleavage mitosis are egg-derivatives. The well-known researches of Fol, Guignard, and Conklin, even if they are not complete enough to prove the theory of the "quadrille," certainly indicate that the egg-centrosomes have a considerable degree of persistence.

Furthermore, it is difficult to demonstrate that the "sperm-centrosomes" are actually brought into the egg by the spermatozoön, and caution must be exercised in referring the origin of the sperm-centrosomes to this source.

Just how the entrance of the sperm revives the latent activity of the oöcyte is not yet fully understood, but the phenomenon is suggestive in that it shows that it is neither the mass of the cell, nor the abundance of yolk, nor the position of the cell, nor the presence of the centrosome that determines the time or rate of cell-division, but that a *stimulus* is required analogous, perhaps, to that which starts into activity the motor apparatus of pigment-cells, leucocytes, or muscle-cells. Following out this suggestion, I have made some experiments upon the unfertilized egg of Chaetopterus.[1]

Watasé has pointed out that the "mechanism of protoplasmic motion" in the leucocyte, pigment-cell, and muscle-cell is similar in its essential features to that in a blastomere during mitotic division (Fig. 5). The aster in the leucocyte and the fibrils, contraction-bands, etc., in the muscle-cell are, most of

[1] I am glad to acknowledge the valuable suggestions and kind assistance of my friend, Mr. C. W. Green, of Johns Hopkins University.

them, permanent features of these cells, persisting even when the cells are at rest. In the dividing cell the corresponding structures are, as a rule, only transitory. The primary oöcyte of Chaetopterus, however, is a remarkable exception to the rule. So long as the oöcyte remains in the body-cavity of the worm, it contains a large germinal vesicle and no trace of asters or centrosomes; but, after it has been deposited in sea-water, a typical amphiaster with distinct centrosomes at either pole is developed. If the egg is not fertilized, the amphiaster

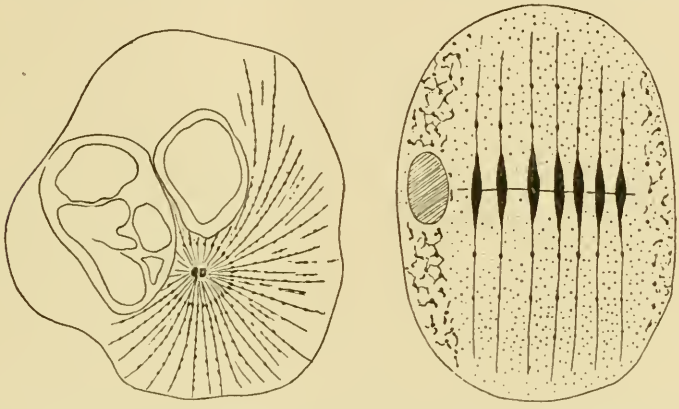

FIG. 5. — Diagram of the motor apparatus in the leucocyte and in the muscle-cell (after Watasé).

on reaching the metaphase (Fig. 4, *B*) remains in this stage for hours, resembling in persistence, as well as in structure, the motor apparatus of leucocytes and muscle-cells.

The leucocyte, as is well known, is susceptible to chemotactic influences; certain chemical substances, *e.g.*, those elaborated by bacteria, will stimulate the motor mechanism of this cell to *normal* activity. Likewise, as Mr. Green has proved, isolated portions of the turtle's heart will resume the normal rhythmical contractions upon the introduction of extremely weak solutions of certain salts; *e.g.*, sodium, calcium, potassium and magnesium. May not the analogous mechanism within the oöcyte of Chaetopterus be induced to resume its normal activity upon the introduction of a similar stimulating substance ?

If this oöcyte, in which the maturation spindle has been developed, is placed in a solution of from ¼ % to ½ % KCl in

sea-water, *the normal mitotic activity is immediately resumed.* The maturation processes, including the extrusion of the first and second polar globules and the concomitant changes in the form of the egg, succeed one another with the same regularity that obtains when the egg is fertilized. In both instances the egg, at first spherical, becomes flattened at the animal pole just before the first polar globule is formed, but soon regains

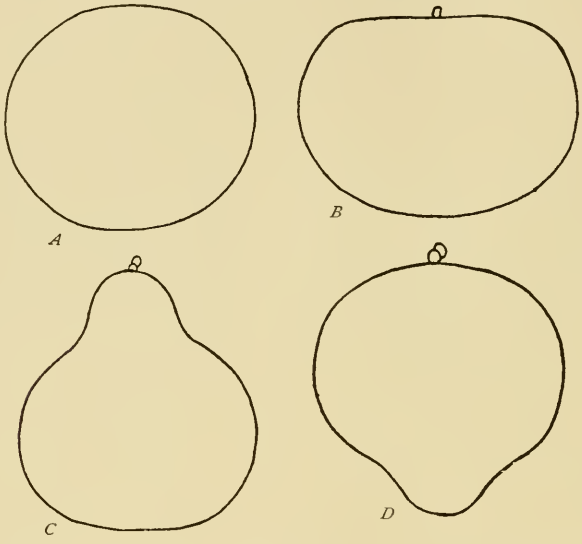

FIG. 6. — Diagram showing some of the changes in the form of the oöcyte and egg-cell which take place upon the entrance of the spermatozoön or upon the addition of potassium chloride to the sea-water. *A*, primary oöcyte before the first polar globule is formed; *B*, secondary oöcyte flattened at the animal pole, first polar globule; *C*, shape assumed when the second polar globule is formed; *D*, formation of the yolk-lobe. (These form-changes are not so pronounced in eggs taken from animals which have been removed from their tubes and have been kept for a few days in an aquarium.)

its original form. About the time the second polar globule is formed, the contour again changes and the egg becomes pear-shaped, the apex towards the animal pole. After this the egg again assumes the form of a sphere (Fig. 6).

But the similarity between the behavior of the fertilized eggs and those subjected to potassium chloride does not stop here, for the "yolk-lobe," a protuberance at the vegetative pole, is formed in both in essentially the same manner. In the fertilized egg, however, the first cleavage-furrow cuts the egg into

two blastomeres, while the lobe is developing, and the latter is borne upon the larger of the two cells, into which it is afterwards resorbed. On the other hand, in the unfertilized egg stimulated by the salt, the lobe, though it is formed in exactly the same manner, is resorbed into the undivided egg, which then once more resumes the form of a sphere. Occasionally a furrow cuts deeply into the egg at the animal pole and then vanishes again, and eggs are found which have every appearance of being in the 2-cell stage.

In regard to the effect produced by the potassium chloride, I wish to emphasize two points: first, it is of the nature of a stimulus, compatible with the continuance of the normal developmental processes, and is not of the nature of a poison or an irritant setting up irregular, abnormal, and inconstant changes; second, the stimulus must be referred to the specific properties of the salt and not to a change in the density of the water in which the eggs are placed. (1) If the unfertilized eggs are allowed to remain in the potassium chloride solution for only a few minutes and are then returned to normal sea-water, the effect is the same as though they were left permanently in the salt solution. Furthermore, eggs may be fertilized in the potassium chloride solution and reared to free-swimming trochophores without being returned to the normal sea-water. (2) If sodium chloride is added to the sea-water instead of potassium chloride, no apparent effect is produced upon the oöcyte; but, if the potassium is added to this solution, or, if spermatozoa be introduced, the polar globules will be formed in the usual manner. Similarly, if the sea-water is diluted by the addition of ⅓ volume distilled water, no effect is produced; but, when the usual amount of potassium chloride is added, the mitosis is immediately resumed.

The behavior of the unfertilized eggs that have been stimulated by the salt is interesting in that it shows how many of the cytokinetic and karyokinetic changes, which are initiated by the entrance of the sperm, are independent of the sperm-nucleus, "sperm-centrosomes," and asters. In the fertilized egg, while the polar globules are being formed, asters are developed about the sperm-centrosomes. These asters grow con-

tinuously and a spindle develops between them, so that by the end of the maturation-period the egg contains a huge amphiaster with extensive rays. The recession of the egg-nucleus appears to be influenced by the presence of this amphiaster and the sperm-nucleus. The development of the yolk-lobe would seem almost certainly to be correlated with the development of the cleavage-amphiaster, since the various phases in its growth and resorption correspond with the definite phases of the cleavage mitosis. Nevertheless, in the unfertilized eggs stimulated with potassium chloride the two maturation-divisions, the reconstitution of the egg-nucleus and its inward migration, and even the protrusion and resorption of the yolk-lobe, take place in the constant and orderly sequence which is characteristic of the fertilized eggs, though there is nothing in them corresponding to the sperm-nucleus or sperm-centres. In the one case, when the yolk-lobe is formed, the egg contains an enormous amphiaster; in the other, no amphiaster or radiations are present.

Although the unfertilized egg will remain in the normal sea-water for several hours without apparent change of form and without loss of the capacity for maturation and fertilization yet, if it is stimulated with potassium chloride, not only do the phenomena of maturation ensue, but, after about an hour and a half, the egg begins to break up into more or less irregular segments, which frequently resemble the ordinary cleavage-blastomeres. The karyokinetic activity *sensu strictu* does not stop with the reconstitution of the egg-nucleus; but, though the sperm-nucleus, amphiaster, and centrosomes are absent, the nine constituent chromosomes divide and the daughter-chromosomes swell up into vesicles which usually remain in one cluster or are irregularly scattered about, and resemble those found in the telophase of ordinary mitosis. At this stage, however, the egg is no longer devoid of radiations. On the contrary, an enormous system of fibers radiates from the centrosphere, which surrounds the group of vesicles and extends in all directions to the periphery. The rays have the appearance characteristic of normal mitosis when the chromatic vesicles have reached this particular stage of development. Not infrequently, when by

virtue of a favorable distribution of the chromosomes these cytoplasmic rays converge towards one point, a dark body — centrosome — may be seen at the point of convergence.

These experiments show that a chemical stimulus, applied for a short time to the oöcyte in Chaetopterus, initiates a series of mitotic changes which extends over a much longer period. The maturation-divisions, reconstitution of the egg-nucleus, and extrusion of the yolk-lobe occur exactly as though the sperm had entered the egg. It is a natural inference from these phenomena that, in normal fertilization, the entering sperm stimulates these mitotic activities in a similar manner, *i.e.*, by exerting a chemical influence upon the egg and not by furnishing the egg with special organs of division. Indeed, the cytokinetic changes, including the formation of the centrosome, seem rather to be in response to the activity of the nucleus than *vice versa*.

This is the more plausible interpretation of those cases in which the entering sperm initiates mitotic division without the participation of the "sperm-centres." According to Wheeler, no middle-piece or centrosome can be distinguished in the sperm of Myzostoma, though the latter initiates the normal mitosis in the egg exactly as it does in Chaetopterus. Moreover, even in the egg of the sea-urchin, Richard Hertwig has shown that strychnine stimulates the production of asters and even of an amphiaster, although he finds no centrosome.

In the egg of Chaetopterus, which has been stimulated by potassium chloride, two consecutive mitoses are completed in the normal fashion, and the abnormal phenomena commence only after the reconstitution of the egg-nucleus. The abnormalities may, perhaps, be referred to the lack of sperm-chromosomes, which are necessary to complete the full number in the cell. That the full number of chromosomes is essential to normal cell activity is attested by its constancy in all tissue-cells and by the universal occurrence of "reduction" before fertilization. The continuance of the cell-divisions in the parthenogenetic eggs of Artemia is also, perhaps, due to the fact that the chromosomes of the second polar globule remain in the egg, rather than to the fact that the centrosomes persist.

From our new point of view we may briefly reëxamine the rate of cell-division in the cleavage-blastomeres.

Let us take, in the first place, as a specific example, one of the prototroch-cells of Amphitrite (Diagram I). It would be difficult to maintain that this cell is unable to divide because of the absence of a vigorous centrosome, inasmuch as it must inherit this structure as an heirloom from the previous cells in whose mitosis there was no indication of waning activity. The inhibition of the division of the prototroch-cell would seem not to depend upon its position, nor upon the absence of an organ of division, but upon the metabolic activity peculiar to the cell by virtue of its internal structure.

The blastomeres adjacent to the prototroch-cells have a different structure, and consequently a different metabolic activity, one expression of which is a difference in their rate of cleavage.

We would not imply that the rate of cleavage of the blastomeres is unaffected by stimuli from without the cell, coming from intercellular secretions, from the medium in which the egg lies, or from some other source; indeed, the effect of potassium chloride upon the oöcyte and egg-cell is evidence to the contrary. The position occupied by one blastomere may be more favorable for the reception of these stimuli than that occupied by another; yet the extreme differences in the rate of division exhibited by cells which are adjacent in time or in space are out of all proportion to the differences in their positions.

The peculiar organization of the cell determines the character of its response to a stimulus — determines whether the cell shall or shall not divide.

TENTH LECTURE.

COALESCENCE EXPERIMENTS UPON THE LEPIDOPTERA.

HENRY E. CRAMPTON, Jr.

The subject of animal-grafting, or the production of coalescence between individuals or parts of individuals, has recently been placed among the most important of modern biological problems by the admirable studies of G. Born upon the embryos of amphibia. It had already been shown by the work of Trembley and, more recently, of Wetzel, upon *Hydra*, and by that of a student of Korschelt, Joest, upon *Lumbricidæ*, that portions of two different animals could be made by proper means to coalesce perfectly. Born, however, was the first to make full demonstration in this regard of the powerful formative energy of embryonic tissue, which is so much greater than the mere regenerative capacity of adult tissues.

By carefully cutting in two frog and toad embryos at the stage when the head and tail are being marked off from the trunk, and by placing the wounds of the fragments in contact, keeping them together by bits of silver wire laid against and across them, Born was able to produce some most interesting and almost grotesque monsters. Two tadpoles united belly to belly with a common liver, a head fused to the belly or back of a complete tadpole, tadpoles cut in half and halves exchanged, tadpoles united head to head — these are some of the unique products of Born's experiments.

The fusion processes of the internal organs and tissues in these cases are of extreme interest. Born found that when

two fragments were united, if similar cells or cells destined to form similar tissues were in juxtaposition, the tissues of the more developed complex showed a perfect union across the wound. This was the case with every kind of tissue except in the notochord, where a break sometimes occurred at the line of the wound. For example, in a belly to belly union the liver cells of one tadpole being in contact with those of the other, a common liver would be formed in the older complex. The same was true for the nerve cord where an anterior half of one embryo was joined to a posterior half of another embryo, in normal proportions; a complete spinal cord resulted. Where, on the other hand, different kinds of cell masses were in contact, only a connective-tissue union occurred; when, for instance, a head was fused to the belly of a complete tadpole, its well-developed neural cord ended abruptly, although connective-tissue cells formed a connection with the tissues of the major component.

Owing to the interest aroused by Born's results, the writer endeavored to find another group of animals which would permit of similar experimenting. Fortunately, the Lepidoptera suggested themselves. Success was anticipated from the outset on general grounds, for the pupa of the Lepidoptera affords an easily handled, quietly growing stage and one which possesses for the production of the imago within the pupal case all the tissue-forming energy of an embryo. Furthermore, beside the possibility of coalescence between two individuals or parts of individuals, other very interesting lines of work appeared; namely, those bearing upon the production of the often wonderful coloration of the wings. It had been shown by the work of A. Mayer and others that the pigmental, as opposed to the structural, colors in the wings of moths are produced by the chemical decomposition of the hæmolymph in the empty scale cells. If, therefore, two pupæ belonging to differently colored species of moths could be made to grow together and produce a pair of coalesced imagines, it would not be unreasonable to expect from the mixed hæmolymph at least some sort of abnormal coloration, if, indeed, there did not appear an actual color effect of each upon the other. Further support

for this assumption was found in the recorded instances of hermaphrodite moths where dimorphic sexual coloration occurred. Such a specimen, one of *Saturnia io*, the writer has seen at the American Museum of Natural History in New York. In this specimen the wings of one side are colored like those of a male, those of the other like those of a female. Oddly enough, the antennæ and legs are correspondingly different in form. The interesting feature, however, is this: that the orange color of the male is clouded by a faint purplish overtone, and the dull female colors are considerably lightened by a yellowish tinge. In other words, the male colors are affected by the female half, and *vice versa*.

The problem of heredity involved is the question whether the color and the gonad of a certain sex are both the effects of a common set of causes, or whether the color is more directly dependent upon the presence of a gonad of a certain sex. As the color is produced by a chemical decomposition of the hæmolymph, and as the hæmolymph can hardly escape being reciprocally affected chemically by the sexual organ that it bathes, the second of the above possibilities would appear to be indicated. The relation of these experiments to the subject of internal secretion, recently put forward by Mathews, is quite obvious. However, the data at present available are not sufficient to warrant any hard and fast conclusion.

The pupæ used in my experiments were those of *Philosamia cynthia*, *Samia cecropia*, *Callosamia promethea*, and *Telea polyphemus*, all belonging to the family Saturniidæ. At first, during the months of February and March, all experiments were performed upon *cynthia*, in order to ascertain if any fusion at all were obtainable. As the operated pupæ in some cases continued to live, success was reasonably assured and the other species were then obtained, although in small numbers, in order to determine the other facts; *viz.*, the possibility of reciprocal color effect upon each other of different species and of different sexes. These latter pupæ, however, had been brought indoors at various times during the winter and spring, and were consequently at different stages of advancement — a fact which materially lessened the chances of successful fusions.

In performing an operation, a strong, very sharp cartilage knife was used. With a single clean cut a portion of a pupa was cut away, and the remainder laid down with the wound uppermost in order to prevent the escape of haemolymph while the second component was prepared. The wounds of the two fragments or components were then placed together, and melted paraffine was applied to the edges with a camel's hair brush. The paraffine on hardening formed a firm ring or band which served the double purpose of keeping the component parts together and of preventing the escape of hæmolymph. Wherever possible the operated complex was suspended in the normal upright position, in cocoons cut to fit.

When in the successful cases the imagines were ready to emerge, a state indicated by the looseness and dryness of the papery pupal shell, it was necessary in almost every instance to pick off the shell with a forceps, bit by bit. A few moths came out independently. In either case the freed moths were put in a box lined with netting, allowing them free room for movement and expansion of their wings. Usually the wings failed to expand to their full normal extent, probably owing to the inevitable loss of hæmolymph during the operation. Sometimes the wings of one component expanded, while those of the other did not, depending apparently on the further development of one beyond the other.

No attempt was made to feed or rear the moths. After being allowed to live a few hours or days, they were chloroformed and dried for total specimens or preserved in spirit. For sectioning purposes some were preserved in Perenyi's fluid and in Graf's chrom-oxalate mixture.

The results fall naturally into three groups, according to the operation and the relative size and make-up of the compound. First, we shall consider those operations where portions of two different pupæ were united in normal proportions. In all cases attempts to join *lateral* halves of two different pupæ were unsuccessful. Here the section passed sagitally a little to one side of the median line. Although many of the compounds lived in a plump, healthy condition for several weeks, all ultimately died.

Better success was attained in joining an anterior end of one pupa to a posterior end of another. Here the section was made completely across the body just back of the posterior ends of the wing cases. Altogether, sixty-one operations of this kind were performed, affording but four living imagines. A compound pupa of this kind is shown in Fig. 1, *a*. Both parts were from *cynthia* pupæ. Three out of twenty-one *cynthia*

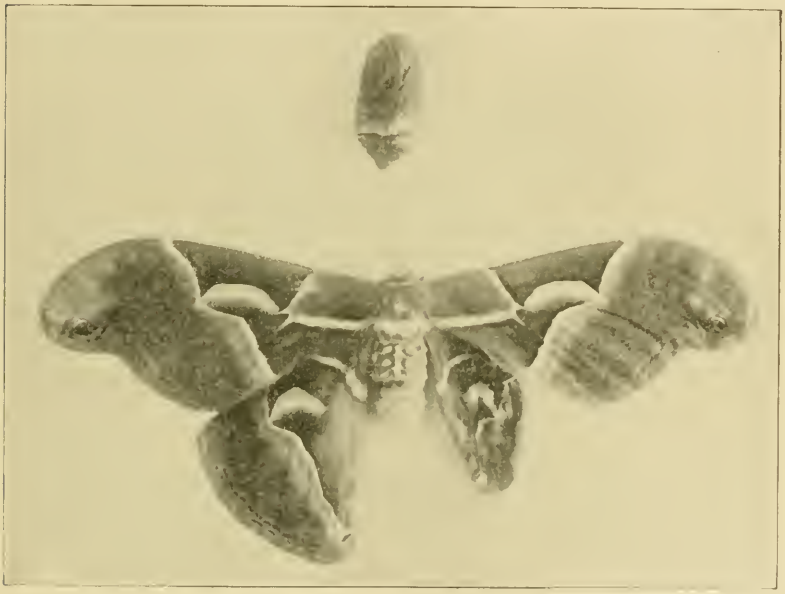

FIG. 1. — Operation of the first category. *a*, compound pupa; *b*, compound moth of *P. cynthia*.

cases furnished moths, two of them emerging unassisted and expanding their wings. One of these is also shown in Fig. 1, *b*. To a casual observer this specimen would appear quite normal. The differences in general color and pattern between the anterior and posterior parts of the abdomen are so slight as to be easily overlooked. A rather curious condition appears in the specimen. The posterior part of the abdomen was taken from a male pupa, while the rest of the body was that of a female. The result is that the eggs contained in the female portion were too large to pass out through the male passages, and a

considerable bulge, noticeable even in the photograph, was caused between the two portions of the compound abdomen.

Altogether, thirty-two attempts were made to unite in normal proportions fragments from two different species; only one was successful. A hinder portion of a *promethea* was perfectly coalesced with an anterior part of a *cynthia*. This specimen is shown in Fig. 2. Apparently, a perfect moth with unexpanded wings confronts the observer. The contour of the abdomen shows no break whatever. A point to be particularly noticed is that the part of the compound abdomen taken from the

FIG. 2. — Operation of the first category. Compound moth, wings, and anterior body from *cynthia*; terminal abdominal segments from *promethea*.

promethea shows no trace of a red color, but is buffy, exactly as the general ground color of the rest of the abdomen, that of the *cynthia*.

Summarizing, then, the results of the operations belonging to this category, we find that out of twenty-nine cases where the parts belonged to pupæ of the same species, three imagines were obtained. Where the fragments belonged to different species, one out of thirty-two gave successful results.

A second group comprises the operations where a compound of two pupæ in "tandem" was prepared; that is, the posterior part of the abdomen of one and the anterior part of the body of another pupa having been sliced off, the remaining fragments were joined on a long axis. Usually the abdomen from the fourth to the terminal segment was cut away from the anterior component, but in some cases the section was made as far back

as between the seventh and eighth segments. The section in the posterior component varied within narrow limits, sometimes passing far back of the eyes just anterior to the roots of the wing cases, sometimes being anterior to the eyes. In many cases, where but a little was sliced off, the posterior component, especially if far advanced, simply healed over its own wound and emerged independently, without the slightest attempt to coalesce with its fellow pupa. Five operations of this kind were made upon *cynthia*, with one successful coalescence. This specimen is of the greatest interest. Unfortunately, a photograph illustrating the important details cannot be taken, and hence no illustration can be given. The interest lies in the fact that from the posterior pupa of the "tandem" were cut away the entire head, — eyes, brain, and all, — the basal portions of the sacs of the antennæ and mouth parts, as well as a portion of the prothorax. The result is that in the coalesced moths *all of these parts are absent.* The weakly developed antennæ and mouth parts of the hinder moth arise directly from the narrow circular sheet of regenerated tissue which spreads from the last abdominal segment of the anterior component to the remains of the prothoracic ring of the posterior component. The microscopic study of the internal conditions of this double specimen will assuredly furnish some very interesting data.

The experiments of this group which would have been of the greatest value, if successful, were those where male and female *promethea* were united. Out of six operations not one gave results, and hence no data for the determination of reciprocal color effect could be here obtained.

Union of *cynthia* and *promethea*, however, gave out of sixteen cases two remarkably fine fusions. One of these is shown in Fig. 3. The components were both female, the *promethea* being posterior. Unfortunately, the wings of both failed to expand, although the moths lived for five days, until chloroformed. The other case was that of a female *cynthia* anterior most firmly united to a *promethea* male posterior. The moths of this compound also failed to expand their wings.

These two cases do not furnish any very definite data bearing upon the color question. It is true that in the first case

there appears on the left posterior wing of the *cynthia* an orange area from which the black scales are absent. Again, the *promethea* is of a slightly lighter red than usual. In the second case, moreover, both components are typically colored, except that the body of the *promethea* shades posteriorly into red, a characteristic color of the female only. Whether these departures from the normal coloration are due to abnormal

FIG. 3. — Operation of the second category. Union in "Tandem" of *P. cynthia*, anterior, and *C. promethea*, posterior.

conditions resulting from the severity of the operations, or whether they are produced by the mixture of the different hæmolymph, is not sufficiently clear.

The third group of operations is that producing "twins." In these cases but little of either pupa was removed, so that two practically entire moths, fused in various ways, result. Sixty-nine pairs, altogether, were prepared, and fourteen of these survived the metamorphosis.

Taking the divisions of this group in order, the first to be noticed are the "head to head" unions. The pupæ were sec-

tioned, as were the posterior components of the preceding series. The resulting moths in the successful cases were fused by their heads; where the section passed a little further back, the prothorax was involved. Four successful fusions were obtained between *cecropia* and *cynthia*, exhibiting, however, no abnormal colors in any of the components. One pair of *cecropia* was perfectly coalesced. Another pair of *cynthia* perfectly united presents a remarkable condition of the antennæ. The left antenna of one component arises from a com-

FIG. 4. — Operation of the third category. *a*, united pupæ, and *b*, united imagines of *S. cecropia*.

mon stem with the right antenna, — that on the same side of the complex, — of its fellow component. The fusion is so intimate that the basal portions of the two antennæ have fused for a distance of over an eighth of an inch.

By cutting away some of the posterior segments of the abdomen it is possible to produce "tail to tail" unions. Two pairs of *cynthia* and one of *cecropia* were able to transform into coalesced moths. Here, again, the internal relations will undoubtedly present conditions of unusual interest.

Siamese twins, united back to back, were produced in but one case. The dorsal portions of the pupal abdomina were cut away. A united pair of pupæ is shown in Fig. 4. The result-

ing moths, a very good pair by way of illustration, show a broad bridge of union extending over the abdominal region from the first to the fourth segments.

Two individuals united by their dorsal thoracic regions are shown in Fig. 5. The posterior ends are turned in opposite directions. This specimen, of no very great interest otherwise,

Fig. 5. — Operation of the third category. *a*, united pupæ and *b*, united imagines of *S. cecropia*.

illustrates the non-expansion of the wings of one moth, while those of the other were of almost the normal extent.

Two moths can be fused by the wings by exposing the roots of the pupal wing cases and uniting the wounds. In the one successful case obtained both moths failed to extend their wings, and no observations upon flight could be made.

In conclusion, it has been shown that it is possible to produce, by placing and keeping together the wounds of two sectioned pupæ or fragments of pupa, a very intimate coalescence between the components. This coalescence is dependent upon

the regenerative or wound-healing power of the tissues involved. So great is this power that in a "defect" *cecropia* example, where the abdomen had been cut away back of the fourth segment and a paraffine film thrown across, the entire wound was covered by a continuous and tough skin. This wound was a half an inch or more in diameter.

It is more difficult to bring about a coalescence between fragments of pupæ belonging to different species or genera than where the two components belong to the same species. Out of 62 operations of the former category 7 cases resulted favorably, about 11.2 per cent. From 95 operations of the second kind, 14 were successful, a percentage of nearly 15. The total number successfully brought through the metamorphosis was 21 out of 127 operations.

Considering the results in another way, the mortality among the pupæ of the first group described, — parts united in normal proportions, — was greatest, the survivors being but 4 out of 61 — 6.5 per cent of the whole. The "tandems" come next, with a total of 3 successes and 24 failures, — 11.1 per cent; the "twins," as would be expected, present the most favorable figures, 14 out of 69, — 20.2 per cent, — pairs affording coalesced imagines.

In regard to the second point, namely, the possibility of reciprocal color effect, the results are somewhat disappointing. With the exception of the two cases of *cynthia* and *promethea* fusion, no departures from the normal color occurred. In none of the cases of twin fusion of two specifically different moths was there the slightest indication of abnormal coloration. The entire question, therefore, as to whether a true reciprocal color effect can be produced awaits the verdict of future extensive experiment.

ELEVENTH LECTURE.

SOME OF THE FUNCTIONS AND FEATURES OF A BIOLOGICAL STATION.[1]

C. O. WHITMAN.

I HAVE a few considerations to offer on a subject not quite new, but perhaps not without some interest to a society of naturalists. The subject may be stated in the form of a question: What are some of the more essential functions and features to be represented in a biological station? This question is one that may fairly claim the attention of a society organized for "the discussion of methods of investigation and instruction, and other topics of interest to investigators and teachers of natural history; and for the adoption of such measures as shall tend to the advancement and diffusion of the knowledge of natural history."

I know of no other organization in this country in which the different sides of biology are more fully and widely represented, and no other in which the discussion of such questions as I have stated has been more explicitly invited.

The question before us, as you perceive, is one of ideals,—something which we can construct without the aid of an endowment, and probably without any permanent loss of protoplasm. And yet, what I have in mind is not wholly imaginery, for it has some basis in experience and in acquaintance with some of the best models.

Let us first of all try to get at some general principle which may serve to guide our judgment of ideals, and by the aid of which we may be able to formulate an answer to the question proposed.

[1] Presidential address prepared for the Ithaca meeting (1897) of the Society of American Naturalists.

As all will allow, ideals are absolutely indispensable to progress and always safe, provided they are kept growing. Like all biological things, live ideals originate by germination, and their growth is subject to no limit except in mental petrifaction. Growth and adaptability are as natural and necessary to them as to living organisms. Here we have, then, an unfailing test for the soundness or relative merit of ideals. Seeds may be kept for years without sensible change or loss of power to germinate. But it is because they are kept, not planted and cultivated. Once planted, they must grow or rot. So it is with ideals. The unchanged ideal that we sometimes hear boasted of is at best but a dormant germ, not a plant with roots and branches in functional activity. If an ideal stands for anything which is growing and developing, then it must also grow, or be supplanted by one that will grow. It is easy, of course, to conceive of ideals a hundred years or more ahead of possible realization; but such ideals could have no vital connection with present needs, and long before the time of possible realization, they would cease to be the best, even if the best conceivable at the start.

We are here, then, concerned only with ideals rooted in experience and continually expanding above and in advance of experience. The moment growth ceases, that moment the work of the ideal is done. Something fails at the roots, and you have waste mental timber to be cleared away as soon as possible to make room for the new seed.

Let us here take warning of one danger to which we are all liable, — the danger of adopting ideals and adhering to them as finalities, forgetting that progress in the model is not only possible, but essential to progress in achievement. The danger is all the greater in the case of ideals lying outside our special field of work, which we are unable to test and improve by our own efforts. The head may thus become stored with a lot of fixed mental furniture, and the possessor become the victim of an illusion, from the charms of which it is difficult to disenchant him. He falls into admiration of his furniture, taking most pride in its unchangeableness. It was, perhaps, the best to be found in the market at the time of installment, and

he finds pleasure in the conceit that what *was* the best is and must remain the best. He sees new developments in the market, but his pride and inertia content him with the old. The illusion now takes full possession of him, and every departure from his new ideals seems like abandonment of the higher for the lower standard of excellence. His conceit grows instead of his ideals, and every annual ring added to its thickness renders it the more impervious.

Can any one say he has never met this illusion? Then a warning may have more pertinency than I should have ventured to claim for it.

To conclude these introductory remarks, let me again emphasize the all-important qualification of the sound ideal and name the prime condition of its usefulness. The qualification is vitality and the capacity for unlimited growth and development. The condition is absolute freedom for growth in all directions compatible with the symmetrical development of the science as a whole. Please remember that the question of means does not now concern us. We must first get at principles, leaving details of execution to be worked out afterwards in harmony therewith. No one can foresee what means may be found, and it would be a waste of time to try to decide what should be done under this, that, or the other set of conditions. If we know our ideal, we know the direction of effort, and through the effort, the means are eventually found.

It will help us in the formulation of our ideal if we glance a moment at the ideals that have found most favor. The best models of marine laboratories ten years ago all agreed in making research the exclusive aim, and in limiting the work to marine forms. In most cases the work was still further limited, embracing only marine zoölogy, and often only a small portion of that field. The idea of representing all branches of even marine biology was seriously entertained nowhere except at Naples. Remembering that marine laboratories were first introduced only about a quarter of a century ago, we are not surprised at these limitations. Even the narrowest limitations were extensions beyond what had been done before. The Naples station itself began as a zoölogical station, and still

bears the name *Stazione Zoologica*. But the earlier ideal was not long in expanding so as to include both physiology and botany. Will its growth stop there? I do not believe it will, but that remains to be seen.

Our own seaside schools, introduced by Louis Agassiz at Penikese and continued by Professor Hyatt at Annisquam, combined instruction with research, and this plan was adopted at Wood's Holl in 1888. Instruction, however, was accepted more as a necessity than as a feature desirable in itself. The older ideal of research alone was still held to be the highest, and, by many, investigation was regarded as the only legitimate function of a marine laboratory. Poverty compelled us to go beyond that ideal and carry two functions instead of one. The result has been that some of us have developed an ideal of still wider scope, while others stand, as they began, by their first choice.

We have, then, two distinct types of ideals, the one including, the other excluding instruction. One is preferred for being limited to investigation; the other is claimed to be both broader and higher for just the contrary reason, — that it is not limited to investigation. At first sight it might seem that we had exact contraries; but that is really not the case, for one type actually includes the other, and differs from it only by the *more* which it contains. The difference is, nevertheless, an important one, and as it divides opinion, we must examine it.

To my mind nothing but experience can settle such a question; but if reason and experience coincide, so much the better, so we may consider it from both points of view. On the basis of ten years' experience and a previous intimate acquaintance with both types, I do not hesitate to say that I am fully converted to the type which links instruction with investigation; and I believe that many, if not most, of my colleagues in the work at Wood's Holl would now concur with me in the opinion that we could not wisely exclude instruction, even if made free to do so by an ample endowment. Some of you will probably feel that such a conclusion implies a step backward rather than forward. On which side is the illusion? Is it with those who have accepted their ideal secondhand and held to it unchanged

from the time of its adoption, or with those who have been compelled to develop their own ideal from all that they could learn by actual experiment and study? Which is the broader ideal, and with which are the possibilities for progressive growth least limited?

In what consists the argument for limitation to research? I have yet to learn of a single important advantage which is necessarily dependent upon this limitation. Is instruction a burden to the investigator, which interferes with his work? That objection is frequently raised, and it is about the only one that we need stop to consider here. That instruction interferes with investigation when it is so arranged as to absorb all or the larger share of one's time no one will deny; but is it not easy to so divide the time that the investigator will find rest and improvement from the instruction he gives? Certainly it is possible, as we have fully demonstrated at Wood's Holl, and that, too, with only the most limited means. With a laboratory open throughout the year, the investigators connected with it would scarcely feel a few weeks' instruction as an impediment. Not only have we shown that such an accommodation or adjustment of functions is possible and tolerable even in our vacations, but we have also learned that there are some important advantages growing out of it which are impossible under limitation to research. To my mind these advantages far outweigh any and all possible objections.

The advantages that I have in mind are not those of means for running the laboratory, which could be supplied by an endowment, but those which add directly to the progress of the investigator and to the advancement of his work. If important advantages exist in connection with instruction even where there is no endowment, which are not available with an endowment, where instruction is excluded, we can readily make our choice of types.

I suppose no investigator, not even the most confirmed claustrophil, would deny that instruction compels thinking and improves ability to express ideas as well as to describe facts. So does writing; so does investigation itself. True, and if that is to their credit, it must be the same to instruction. But

wherein is the advantage with instruction? Every teaching investigator can answer that; and the answer will be, that power of exposition can be acquired and perfected by class work and lectures to an extent otherwise unattainable. In this we need no better example than Huxley. If rare powers of exposition are sometimes gained without teaching, as in the case of Darwin, that in no way weakens the position here taken, which is that teaching is the most effective method, — not the only one, yet an essential one to the highest attainment.

One thing more on this point. Why do we place so high a value on investigation? Because it is the only way of advancing knowledge, and because it affords a most attractive field for the exercise of the mind. But if knowledge needs advancement, so does the investigator, and whatever contributes to the increase and improvement of his powers makes him the better investigator, and thus indirectly raises the quality and augments the quantity of his researches. Herein instruction plays a very important part, as becomes evident when we remember that with increasing specialization in science the investigator himself becomes more and more dependent upon the instruction which he draws, not only from books and journals, but also directly from his colleagues and his pupils. Indeed, he may learn in this way much quicker and more thoroughly than by reading, and often a long time in advance of publication. That is an immense advantage realized in a variety of ways, as in lectures giving the more important results of work before publication; in seminars where the results of individual investigators are brought forward and discussed, while the work is still in progress; in journal clubs devoted to reviews and discussions; in direct intercourse with pupils, seeing with their eyes and working with their hands; in daily intercourse of thought and comparison of observations with fellow-workers, etc. Indeed, it may be truly said that no one stands in such close and pressing need of continual instruction as the investigator. No one else absorbs it more eagerly and copiously, and no one else can convert it so directly into the results of research.

Another advantage supplied by instruction must be mentioned here, for in it I see opportunities for development of

far-reaching importance to research. It is lamentable to see so much energy available for research lost or ineffective for lack of proper directive coördination. The avalanche of modern biological literature consists largely of scrappy, fragmentary, disconnected products of a multitude of investigators, all working as so many independent individuals, each snatching whatever and wherever he can, and then dumping his heterogeneous contributions into the common hodgepodge. How are we ever to extricate ourselves from such appalling confusion? The ambition to be prolific rather than sound is a peril against which we seem to have no protection at present. And yet, if I mistake not, there is a growing sentiment against such traffic in science, which will eventually make it plain that ambition in that direction spends itself in vain. A dozen or more dumps a year, with as many or more retractions, corrections, and supplements, is only a modest-sized ambition. Conclusions are palmed upon the unsuspecting reader, and then, without compunction or apology, reversed from day to day or from month to month, or, worse still, in an appendix subjoined, so that it may be seen how little it costs to be prolific when one day's work cancels another.

It behooves us to find effective remedies as rapidly as possible. The correction would be complete if each worker could bridle his lust for notoriety and take the lesson of Darwin's industry and reservation into his laboratory and study. The outlook for such a millennial dispensation is not very hopeful, and our resources are few and very inadequate, but all the more deserving of attention. The great need is *long-continued*, *concentrated*, and *coördinated work*. In a laboratory which draws beginners in investigation in considerable numbers, it is possible to assign problems in such a way that the participants may work in coördinate groups, and the problems be carried on from year to year, and from worker to worker, each performing his mite in conjunction and relation with the others of his group. In this way energy would be utilized to the greatest advantage to science, as well as to the individual. Even under the very imperfect conditions represented at Wood's Holl, I have found it possible to put this idea into practice to some

extent, and I have great faith in its efficacy. Herein we see another possibility of development realizable only through instruction.

But it is as important for independent investigators as for beginners to cultivate organic unity in their work. How shall the investigator hope to keep in touch with the multiplying specialities of his science? Here again I maintain that instruction is an indispensable means. Fill a laboratory with investigators and, if no instruction is provided, many of the more important avenues of acquisition will be closed and the opportunities for coördination of work will be of little or no avail. Investigators might work for months in adjoining rooms and never learn anything about each other's work, as every one knows who has worked in such a laboratory. How different in a laboratory where instruction is so arranged as, without overtaxing any one, to bring the workers into active and mutually helpful relations, and enable them to draw from one another the best that each can give! Instruction in the various forms before indicated supplies just the conditions most favorable to interchange of thought and suggestion. It is just this feature of our work at Wood's Holl to which we are most indebted for whatever success we have had.

I am aware that other points might be raised, but it is far from my purpose to run down all possible objections. It is enough to have indicated the grounds of my choice of types. It now remains to briefly sketch the general character and to emphasize some of the leading features to be represented in a biological station.

The first requisite is capacity for growth in all directions consistent with the symmetrical development of biology as a whole. The second requisite is the union of the two functions, research and instruction, in such relations as will best hold the work and the workers in the natural coördination essential to scientific progress and to individual development. It is on this basis that I would construct the ideal and test every practical issue.

A scheme that excludes all limitations except such as nature prescribes is just broad enough to take in the science, and that

does not strike me as at all extravagant or even as exceeding by a hair's breadth the essentials. Whoever feels it an advantage to be fettered by self-imposed limitations will part company with us here. If any one is troubled with the question, Of what use is an ideal too large to be realized? I will answer at once: It is the merit of this ideal that it can be realized, just as every sound ideal can be realized, only by gradual growth. An ideal that could be realized all at once would exclude growth and leave nothing to be done but to work on in grooves. That is precisely the danger we are seeking to avoid.

The two fundamental requisites which I have just defined scarcely need any amplification. Their implications, however, are far-reaching, and I may therefore point out a little more explicitly what is involved. I have made use of the term "biological station" in preference to those in more common use, for the reason that my ideal rejects every artificial limitation that might check growth or force a one-sided development. I have in mind, then, not a station devoted exclusively to zoölogy, or exclusively to botany, or exclusively to physiology; not a station limited to the study of marine plants and animals, not a lacustral station dealing only with land and fresh-water faunas and floras, not a station limited to experimental work, but a genuine *biological* station, embracing all these important divisions, absolutely free of every artificial restriction.

Now that is a scheme that can grow just as fast as biology grows, and I am of the opinion that nothing short of it could ever adequately represent a national centre of instruction and research in biology. Vast as the scheme is, at least in its possibilities, it is a true germ, all the principal parts of which could be realized in respectable beginnings in a very few years and at no enormous expense. With scarcely anything beyond our hands to work with, we have already succeeded in getting zoölogy and botany well started at Wood's Holl, and physiology is ready to follow.

If now experimental biology could be started, even in a modest way, it would add immensely to the general attractions of our work, for it would open a field which is comparatively new and of rapidly growing importance. There are so many

things now called "experimental," that I must explain what I have in mind sufficiently to make the general purpose intelligible.

It is not that experimental embryology redundantly described as "developmental mechanics" which is now in vogue; not laboratory physiology, even in its wider application to animals; not egg-shaking, heteromorphism, heliotropism, and the like, — not any of these things, but experimental natural history, or biology, in its more general and comprehensive sense. It is not the natural history of the tourist or the museum collector or the systematist, but the modern natural history, for which Darwin laid the foundation, and which Semper, Romanes, Varigny, Weismann, Galton, Lloyd Morgan, and others have advocated and practised to the extent of the meager means at their command. The plan which I should propose, however, has not, so far as I am aware, been definitely formulated by any one, although some of its features were indicated several years ago when I proposed such a station in connection with the University of Chicago. The essentials of the plan were sketched as follows:

"Experimental biology represents not only an extension of physiological inquiry into all provinces of life, but also the application of its methods to morphological problems; in short, it covers the whole field in which physiology and morphology can work best hand in hand . . .

"A lake biological station, equipped for experimental work, would mark a new departure for which science is now ripe. Such a station has nowhere been provided, but its need has been felt and acknowledged by the foremost biologists of to-day. There are no problems in the whole range of biology of higher scientific interest or deeper practical import to humanity than those which centre in variation and heredity. For the solution of these problems and a thousand others that turn upon them, facilities for *long-continued experimental study, under conditions that admit of perfect control, must be provided.* Such facilities imply first of all material for study, and that nature here supplies in rich abundance. Then a convenient observatory with a scientific staff is required. In addition, — and this

is all-important, — there should be not only aquaria and plenty of running water, but also a number of ponds with a continuous supply of water, so arranged that the forms under observation could be bred and reared in isolation when necessary. Finally, there should be room for keeping land animals and plants under favorable conditions for cultivation and study. A station with such facilities as have been briefly indicated would furnish ideal conditions for the prosecution of research in nearly every department of biology, and especially in embryology and physiology."[1]

If such a station could be developed in immediate connection with the plant already under way at Wood's Holl, we might begin to realize what a biological station stands for.

We need to get more deeply saturated with the meaning of the word "biological," and to keep renewing our faith in it as a governing conception. Our centrifugal specialities have no justification except in the *ensemble*, and each one of them is prolific in grotesque absurdities, for which there is no correction in disconnection with the organic whole. But why talk of an organic whole, which no man can grasp, or make any pretension to mastering? Precisely that makes it necessary to talk and act as if we knew the fact, and as if our inability had not rendered us insensible to our need. Physiology is meaningless without morphology, and morphology equally so without physiology. Both find their meaning in biology, and in nothing less. What an absurdity was human anatomy without comparative anatomy; and comparative anatomy was only a much bigger absurdity until the general connection of things began to dawn in the conceptions of biology. Just think of a physiologist seriously proclaiming to the world that instinct reduces itself in the last analysis to heliotropism, stereotropism, and the like. The whole course of evolution drops out of sight altogether, and things are explained as if the organic world were a chemical creation only a few hours old. The absurdity would be no greater for a geologist to try to explain the earth without reference to its past history.

Think of a young morphologist, with all the advantages of

[1] Programme of Courses in Biology, Chicago, 1892.

the Naples station at hand, yes, within the walls of that grand station, loudly sneering at Darwinism, and spending his wit in derisive caricatures of general truths beyond the horizon of his special work and thought. And shall we forget the physiologist whose philosopher's stone is the search for his ancestry among the arachnids; or the anatomist who reverses his telescope to discover that his science begins and ends in terminology? And could we, much as we might yearn for such a benediction, forget the omnipresent and omniscient systematist, whose creed is summed up in priority?

The catholicon for crankiness has not been found, but in science there is but one cure where cure is possible; it is exposure to the full and direct rays of the system as a whole. The application to the subject in hand is patent. The one great charm of a biological station must be the fullness with which it represents the biological system. Its power and efficacy diminish in geometrical ratio with every source of light excluded.

My plea, then, is for a biological station, and I believe that experimental biology would be the most important element in such a station. It is now possible to procure a favorable site, with land and fresh-water privileges, in close proximity with the Marine Biological Laboratory, and with a moderate foundation to start with, the work could begin at any moment.

The project is certainly one of preëminent importance, and for a successful undertaking of that magnitude we need the active coöperation of American naturalists. I bring the suggestion before you in the hope that it will enlist your interest and support.